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BIOLOGY, TAXONOMY, AND EVOLUTION OF FOUR SYMPATRIC AGRILUS BEETLES

(COLEOPTERA: BUPRESTIDAE)

by

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INTRODUCTION

Objectives

Beginning in the summer of 1964 we endeavored to study the natural history and taxonomy of four sympatric Agrilus Megerle[1] (Coleoptera: Buprestidae). These Agrilus were of particular interest because of their morphological similarities. Three of them, the bronze birch borer (Agrilus anxius Gory), the bronze poplar[2] borer (A. granulatus liragus Barter and Brown[3]) and the aspen root girdler (A. horni Kerremans) had only been distinguished rather recently. The fourth species, A. pensus Horn (= betulae Fisher) is distinct from the others in coloration, but very similar otherwise. The credibility of contentions that these taxa are very closely allied will be deliberated here in the light of:

1) A taxonomic study of these and related Agrilus, which included working both with specimens and literature.

2) An analysis of their larval habits, their ecological relationships to their hosts, and their population-limiting factors. Much of what is known about these aspects is taken from the literature and reinterpreted in the light of more recent findings, and pertinent writings on other Agrilus are also discussed.

3) Direct and indirect observations on the behavior of the adults in the field and laboratory.

4) A preliminary study of interspecific mating and a theoretical analysis of phylogeny, zoogeography, and speciation (or subspeciation).

Historic Background

THE BRONZE BIRCH BORER. A. anxius is probably the most notorious Nearctic species in the genus, and at one time was thought to be the cause of birch dieback. It was first recognized as a pest of shade trees and ornamental birches in the late 1800's and was called "the bronze birch borer" by Chittendon (1898). Chittendon says that "one correspondent has expressed the belief that if radical measures are not adopted, the loss of every birch in the city of Buffalo in the near future is imminent. This insect has already destroyed the common white birch [Betula papyrifera] and . . . many of the cut-leaf and European white birches. It even attacks trees planted but a year before."

Most of the reports of damage came from the northeastern U. S., perhaps because more birches had been planted there as shade trees. Nevertheless,

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[1] The majority of authors credit Curtis (1825) with originating the name Agrilus. However, Megerle (1823) published a price list in which the heading "Agrilus v. M. Buprestis)" appears. This simple listing credits Megerle with authorship, and Curtis (1825) merely designated one of Megerle's included species, Buprestis viridis L., as the genotype.

[2] The term poplar will here be used to refer to species in all sections of the genus Populus.

[3] Described as Agrilus liragus Barter and Brown (1949); status changed by Carlson (1969).

the problem was not confined to that region. Chittendon (1900), for example, notes that in 1899 "Prof. F. C. Newcombe of the University of Michigan, Ann Arbor, Mich., wrote that what was without doubt this species, and which he designated as the white birch borer, had been in that locality for two or three years and had killed half the white birches in the city of Ann Arbor."

Swaine(1918) first reported *anxius* killing trees in forests. This was the start of a devastating and puzzling epidemic of birch dieback which primarily affected *Betula papyrifera*, although some mortality of *Betula lutea* (=*alleghaniensis*) was also ascribed to this affliction. By 1951, 67 percent of the birches in Maine had been killed, and 15 percent of those remaining were in a decadent state due to the effects of birch dieback and bronze birch borer attack (Nash, Duda, and Gray, 1951).

Much research concerning the bronze birch borer and dieback in the 1940's and 1950's was directed at determining whether or not the beetle was causing the death of the trees. This question was hardly a new one then. Chittendon (1898) says "as in the case of injury ascribed to the two-lined chestnut borer [*Agrilus bilineatus* Weber] there is still a certain question of doubt as to whether or not this birch borer is really the primary cause of the death of the trees. Our correspondent is of the opinion that the injury in Buffalo is due primarily to the attack of this borer, since it has been observed attacking vigorous trees." The work of Anderson (1944), Nash et. al. (1951), and Barter (1957) shows, however, that the insect played a secondary role, usually killing those trees already afflicted with birch dieback. Whether or not birch dieback was the predisposing factor in earlier ravages of the bronze birch borer, when it allegedly killed mostly shade trees, is dependent upon what birch dieback really is. It is evident that the shade trees in many cities were in a weakened condition in the late 1800's, perhaps because of droughtiness.

THE BRONZE POPLAR BORER. The habits of *A. granulatus liragus* adults were first observed and recorded by Lintner (1883) before anything was published about the habits of *A. anxius*, and of course well in advance of the establishment of the fact that the poplar feeder and birch feeder were not one and the same. Chittendon (1898) says, "a very singular thing in connection with the occurrence of this borer in birch is that in spite of frequent search, extending over a period of two years, our correspondent has been unable to find this insect attacking any other tree than birch--a remarkable condition of affairs when we consider the numbers of observations by careful observers of its occurrence on poplar and willow."

Smith (1949a) discovered that the *A. anxius* (*sensu* Fisher, 1928) reared from *Betula* spp. had 22 chromosomes, while those reared from *Populus* spp. had only 20. Subsequently, Barter and Brown (1949) named the poplar feeding form *A. liragus*. Although *A. granulatus liragus* has habits nearly identical to those of *anxius* (host specificity excepted) it has never been accorded any great significance as a pest. Like *anxius* the bronze poplar borer attacks and kills only trees in weakened condition (Barter, 1965). because poplars are used less frequently as ornamentals than birches, *g. liragus* is not as important an ornamental pest as *anxius*. Furthermore, no large scale maladies on the order of birch dieback occur in forests of native North American *Populus* spp. so that the bronze poplar borer has not been associated with forest devastation.

THE ASPEN ROOT GIRDLER. Harrison (1959) discovered what he thought to be a new species of *Agrilus* feeding on the roots of aspen suckers (*Populus tremu-*

loides and *P. grandidentata*). The establishment of a chromosome number of 22 for this species seemed to indicate that it was more closely allied to *anxius* than to *g. liragus* (Nord, 1962). Later, Nord, Knight and Vogt (1965) discovered that the proper name for the root boring form is *A. horni*, a name which Fisher (1928) and Barter and Brown (1949) thought to be a synonym of *anxius*. Because of their uncertainty, however, they did not synonymize *horni* with *anxius*.

A. horni has attained a modest reputation as a pest. Nord (1962) says that it caused severe damage to hybrid aspen out-plantings which were part of genetics experiments conducted by the Institute of Paper Chemistry in Wisconsin and Michigan. In 1964, the trees in some of the affected plots were destroyed and the tests were reinitiated. However, in 1964 they were still having trouble controlling *horni*.[1] This, no doubt, was due to the inappropriateness of the control techniques used, rather than to any factor in the beetle's ecology which makes it difficult to control. Moreover, because of its ecological preferences, it is not likely that this insect will ever cause great injury to well-stocked natural stands of aspen suckers that are growing on areas of moderate or good site quality.

THE ALDER-BIRCH BORER. Fisher (1928) was uncertain of the status of *A. pensus*. He says "this species may only represent a color variety of *anxius*, but since nothing is known of its habits, it is best to retain it for the present, at least, as a valid species." Even though he was unsure of the distinction between *pensus* and *anxius*, he took the liberty of describing *betulae*, a synonym of *pensus*, from 3 specimens. Although there is really little question that *pensus* is actually a distinct species, its biology remained almost unknown prior to the studies here described. The ecology of *pensus* makes it rather innocuous, and it has attracted little attention. However, it appears to be an important factor in the ecology of alders (*Alnus* spp.), which are important as wildlife cover in their lakeside and streamside habitat.

TAXONOMY

The Genus *Agrilus*

SIZE AND DISTRIBUTION. *Agrilus* beetles are thought to feed only on angiosperms (Fisher, 1928). Confinement to angiosperms could indicate that the genus arose in the Cretaceous or later, which seems to allow ample time for it to have attained the vast size and worldwide distribution it presently has. Schaefer (1949) said the genus included 2500 described species, and Obenberger (1957) claimed that in his collection alone, there were over 3000 described and undescribed forms. Obenberger (1959) believed that there are over 4000 species of *Agrilus*.

The largest number of species occur in tropical or subtropical areas, but *Agrilus* is well-represented in temperate regions too. Fisher (1928) recognized 125 described forms from the North American fauna (North of Mexico), and a considerable number have been described since, mostly from the south-

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[1] Personal communication, 1964; D. Einspahr, Institute of Paper Chemistry, Rheinlander, Wisconsin.

western United States.

SUBDIVISIONS. Obenberger (1957, 1959), with some rather specious reasoning, tried to show that there is no way to divide *Agrilus* into acceptable subgenera. He was, however, willing to admit that there are some recognizable species groups.

The economically important Eurasian "species"[1] *Agrilus viridis* L., its many destructive "host races," and the lesser known North American *A. politus* Say together represent such a species group which is extremely difficult taxonomically. Both *A. politus* and *A. arcuatus* Say are classified by Fisher (1928) as being composed of several sympatric "subspecies," but each actually represents a multi-species "complex."

Frost (1912) recognized some of these "sibling species" problems, and presented suggestions for their solution. He concluded by saying "the studies in the *otiosus*[2] and *anxius* groups have been so far, rather dissappointing, due to the difficulty of getting series of both sexes. The only species that is at all abundant in this locality is *otiosus*, taken on oak leaves. The olivaceous variety of *acutipennis* has been encountered quite often on oak, and *bilineatus* occurs in favorable places on oak sprouts, but in general the species turn up singly or in pairs, with aggravating slowness. Several very interesting problems are suggested by the material in hand, and more specimens from widely separated areas may present a solution." In many groups of *Agrilus*, a similar situation still exists.

The *Agrilus anxius* Group

DEFINITION. Presumably broadening the limits of the *Agrilus anxius* group *sensu* Frost (1912), it is here defined as those species in which the adults have the carina of the pygidium projecting as a spine, (figs. 2, 3), and (2) have a sexual dimorphism in the structure of the last abdominal segment. The marginal sclerite[3] of the hind segment is smooth and in males lies in a plane nearly confluent with that formed by the sternite (fig. 33). In females the marginal sclerite is reflexed or beveled with respect to the sternite (fig. 32). In most of the species the first and/or second abdominal sternites are also sexually dimorphic. In males these sternites are often grooved medially (fig. 1), while females never have such a groove.

NOMENCLATURE Nord et al. (1965) have referred to the "*Agrilus anxius* complex." The term complex carries a connotation of propinquity that is inappropriate for a group that includes *anxius*, *g. liragus*, and *horni*, and we,

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[1] Actually includes a number of sympatric species (see, for example, Basurmanova, 1958).

[2] *Agrilus otiosus* Say.

[3] Those parts of the tergites termed the "vertical portions of the segments" by Fisher (1928), but they are not vertical on the hind segments and the term marginal sclerite seems to be a preferable alternative.

therefore, will not apply it here. The *Agrilus anxius* group is comparable to what in many other families of insects would be recognized as a genus. Were the *anxius* group to be delineated from other *Agrilus* as either a subgenus or genus, either of the *Agrilus* synonyms *Teres* Harris (1829) or *Uragrilus* Semenov (1935) (=*Epinagrilus* Stepanov, 1954) could be applied. Because the limits of the *anxius* group are not ascertainable from the literature, it would be unwise to use a formal name for it at this time.

MORPHOLOGIC ANALYSIS . The taxonomic analysis of *anxius* group species is based primarily on adult morphology, but important information is also furnished by other developmental stages. The interpretation of morphologic characters is strongly influenced by studies of adult behavior which are discussed later, and some findings from studies of adult morphology are deferred to the Evolution section.

Adults. The analysis of adult morphology was based primarily on collections made in Michigan (Iron, Gogebic, Benzie, and Manistee Counties) and Wisconsin (Vilas Co.). Material in the collections of the University of Michigan Museum of Zoology (Ann Arbor, Michigan) the Entomology Research Institute of Canada (Ottawa, Ontario), Harvard University, Museum of Comparative Zoology (Cambridge, Massachusetts), the Philadelphia Academy of Sciences (Philadelphia, Pennsylvania) and the U. S. National Museum (Washington, D.C.) was also examined. The following types were studied: *Agrilus betulae* Fisher, *Agrilus fulminans* Fisher, *Agrilus populi* Fisher, *Agrilus horni* Kerremans (=*blanchardi* Horn, name preoccupied), *Agrilus nevadensis* Horn, *Agrilus niveiventris* Horn, *Agrilus pensus* Horn, and *Agrilus gravis* Leconte.

On the basis of the study of the types and other material the following nomenclatural changes (including those made by Carlson [1969]) were called for and will be followed here:

AGRILUS BROWNI, new species

Agrilus browni, new species
Agrilus lateralis, *sensu* Fisher (1928), in part.

Fig. 1. Ventral aspect of *Agrilus horni* ♂, showing the median groove on abdominal sternites 1 and 2.

AGRILUS GRANULATUS Say

Agrilus granulatus granulatus Say
  Buprestis granulata Say (1823)
Agrilus granulatus populi Fisher; status assigned by Carlson (1969)
  Agrilus populi Fisher (1928)
  Agrilus trichocarpae Chamberlin (1929)
Agrilus granulatus liragus Barter and Brown; status assigned by Carlson (1969)
  Agrilus liragus Barter and Brown (1949)

AGRILUS PENSUS Horn

Agrilus pensus Horn (1891)
  Agrilus betulae Fisher (1928); synonymy designated by Carlson (1969)

AGRILUS QUADRIGUTTATUS Gory

Agrilus quadriguttatus quadriguttatus Gory
  Agrilus quadriguttatus Dejean (1833, 1836), nomen nudum
  Agrilus quadriguttatus Gory (1841)
Agrilus quadriguttatus niveiventris Horn; status assigned by Carlson (1969)
  Agrilus niveiventris Horn (1891)
  Agrilus nevadensis Horn (1891); synonymy designated by Carlson (1969)
Agrilus quadriguttatus fulminans Fisher; status assigned by Carlson (1969)
  Agrilus fulminans Fisher (1928)

AGRILUS RUFICOLLIS Fabricius

Agrilus ruficollis Fabricius
  Buprestis ruficollis Fabricius (1787)
  Agrilus lateralis Say (1823), new synonymy
  Agrilus sayi Saunders (1871), name unnecessary (lateralis not preoccupied)

Fisher (1922) reared an Agrilus sp. from bayberry (Myrica pensylvanica, = carolinensis) at Lyme, Connecticut, for which he used the name A. lateralis Say. The original description[1] of lateralis (Say, 1823), however, fits A. ruficollis Fabricius more closely than the species that was reared from Myrica. For that reason and because of the range limits apparent for it, the species which Fisher reared from Myrica is here given the name Agrilus browni n. sp.

Say (1823) says the head of lateralis has a profoundly impressed line, which certainly is characteristic of ruficollis. A. browni has the front only weakly impressed. Say also notes that the length of lateralis is 1/5 inch (about 5.1 mm), which is not exceptionally short for ruficollis, a smaller and more variable species than browni. On the other hand, specimens of browni as short as 5.1 mm must be extremely rare, as we have seen none approaching that size.

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[1] According to Fisher (1928) the lateralis type was lost, but, presumably, it was destroyed, as is the case for the majority of Say's specimens.

The only bonafide records for browni are from places very remote from the lateralis type locality. Say (1823) described lateralis from a specimen collected in Missouri, which then included the vast region west of the Mississippi known as the Louisiana Purchase, excluding what is now the state of Louisiana. Knull (1922) found browni in abundance on sweet ferns (Myrica asplenifolia, = Comptonia peregrina) in Pennsylvania, but no reliable records are known to us for any area west of that state. In spite of the examination of large amounts of sweet fern by P. C. Kennedy[1] and a modest amount of searching on that host plant by us, browni has not been encountered in Michigan. The strength of all the evidence leads us to suppress lateralis as a synonym of ruficollis.

Fisher (1928) provides a good description of browni (under the name lateralis), and his "lateralis" neotype[2] is here designated as the type of browni. The species is named for Mr. William J. Brown[3], who suggested that Fisher (1922, 1928) had misapplied the name lateralis.

Fisher (1928) knew A. nevadensis Horn only from the type, and that specimen appears to have been deformed during pupal development. Fisher (1928) says its scutellum is not carinate, but the carina appears to be present, although it is positioned abnormally on the deformed scutellum. The somewhat prolonged elytra have more sharply pointed apices and more coarsely rugulose surfaces than typical q. niveiventris, but there are no other structural differences. The pigmentation of some specimens of q. niveiventris from southern California is as dark as that of the A. nevadensis type, which was collected in Nevada.

The following sections will be devoted primarily to anxius, pensus, horni, and g. liragus. The discussion of other members of the anxius group is deferred to a later section on evolution.

Since Gory (1841) described anxius, other forms have been named, two of which are synonyms, while another was mistaken for a synonym. Agrilus gravis Leconte and A. torpidus Leconte were described in 1859, but Fisher (1928) placed them as synonyms of anxius. Agrilus blanchardi Horn (not Saunders) and A. pensus Horn were described in 1891. Because the former was a primary homonym, it was renamed A. horni by Kerremans (1900). Fisher (1928) thought that horni was a synonym of anxius. Knowing of no material besides the type which could be identified as horni, he believed that it was merely an abnormal specimen. Being somewhat uncertain, however, he retained horni as valid.

When Barter and Brown (1949) established that a poplar-feeding form and a birch-feeding form had been confused under the name anxius, they decided

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[1] Personal communication, 1967; P. C. Kennedy, North Central Forest Experiment Station, U. S. Forest Service, East Lansing, Michigan.

[2] According to Fisher (1928), this specimen is a male, which he collected on bayberry at Lyme, Connecticut and deposited in the U. S. National Museum collection.

[3] Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario.

to retain[1] that name for the birch-feeding form. They suppressed *torpidus* as a synonym of *anxius*, but made no definite decision regarding the name *gravis*. The *gravis* type is a female that Barter and Brown (1949) could not identify reliably. The name *liragus* was, therefore, given to the poplar feeding form with the distinct possibility of it later proving to be a synonym of *gravis*. There have been doubts that this was the proper thing to do. For example, the application of *gravis* by Blanchard (1889) for the species collected on poplars (not "sprouts"[2]) is cited by Nash et al. (1951) as a possible indication that *gravis* was the proper name for the poplar feeder.

Although the *gravis* type lacks the coppery sheen often found on the head and pronotum of *anxius* specimens, its absence is not a good indication of the identity of the type. Vogt[3] pointed out that specimens of *anxius* from some parts of the Great Lakes Region are often colored more like *g. liragus* than are specimens from more eastern parts of the United States. Indeed, the coppery reflections are often very indistinct in specimens from the Upper Peninsula of Michigan, which lies within the type locality recorded by Leconte (1859) as the "Lake Superior Region."

By relying on characteristics other than coloration and working with specimens collected in the Upper Peninsula of Michigan, we found that *Agrilus gravis* Leconte is really a synonym of *anxius* Gory, and therefore *g. liragus* Barter and Brown is to be retained as valid The name *gravis*, as used in a number of papers in the late 1800's, refers to either *anxius* or *g. liragus*; assignment to one or the other depends upon the host designated, if any. References using the other *anxius* synonym, *torpidus* Leconte, are to be treated similarly, except for those which refer to willow as a host. The latter (e.g. Cook, 1890; Davis, 1891, 1892) refer to *A. criddlei* Frost, which makes galls on willows. The host of *criddlei* was recently established through rearing by Wong and McLeod (1965).

Barter and Brown (1949) concluded that *anxius* and *g. liragus* are separable only by reliance on male genitalia, coloration of the head and pronotum, and host plant identity. We cannot concur with them fully. As previously indicated, *anxius* specimens from some areas do not have very distinct coppery reflections on the pronotum, and this iridescence also seems to fade quite rapidly in some museum specimens. Wetting the specimens with various relaxing agents is particularly destructive to the iridescence of these beetles. On the other hand, there are structural differences, besides male genitalic ones which, in combination, can be used for separating *anxius* and *g. liragus*. One of these, a difference in the form of the tarsal claws, was not noted by Barter and Brown (1949). The membraneous attachment of the tarsal claws of *g. liragus* appears to be either more flexible or looser than that of *anxius*. Consequently, the *g. liragus* tarsal claws are often clearly separated from the unguifer, making the

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[1] They indicated the location of the *anxius* type as being unknown.

[2] Blanchard thought what he had found on poplar sprouts was *anxius*.

[3] Personal commununication, 1966; G. B. Vogt, U. S. Dept. Agr., A.R.S., Entomology Res. Div., Washington, D. C.

latter clearly visible. The claws of anxius are attached so that there is very little space between their bases and the unguifer. The unguifer, is therefore, more difficult to see. In addition, the claws of anxius are usually rather distinctly swollen at their bases, and tend to obscure their attaching membrane which stretches across the opening in the last tarsomere, while in g. liragus the basal parts of the claws are usually not strongly swollen, and the membrane in the tarsomere opening is usually readily visible.

The females of anxius and g. liragus differ in the shape of the projecting spine on the pygidium, but the males do not. In g. liragus females the spine usually projects strongly (fig. 2) and is rather cylindrical, while in anxius females it is usually shorter and more blunt (fig. 3), and its tip is often broad and elyptical in end view.

A useful characteristic mentioned by Barter and Brown (1949), is the tendency for the elytral tips of g. liragus to be acute and strongly serrate (fig.

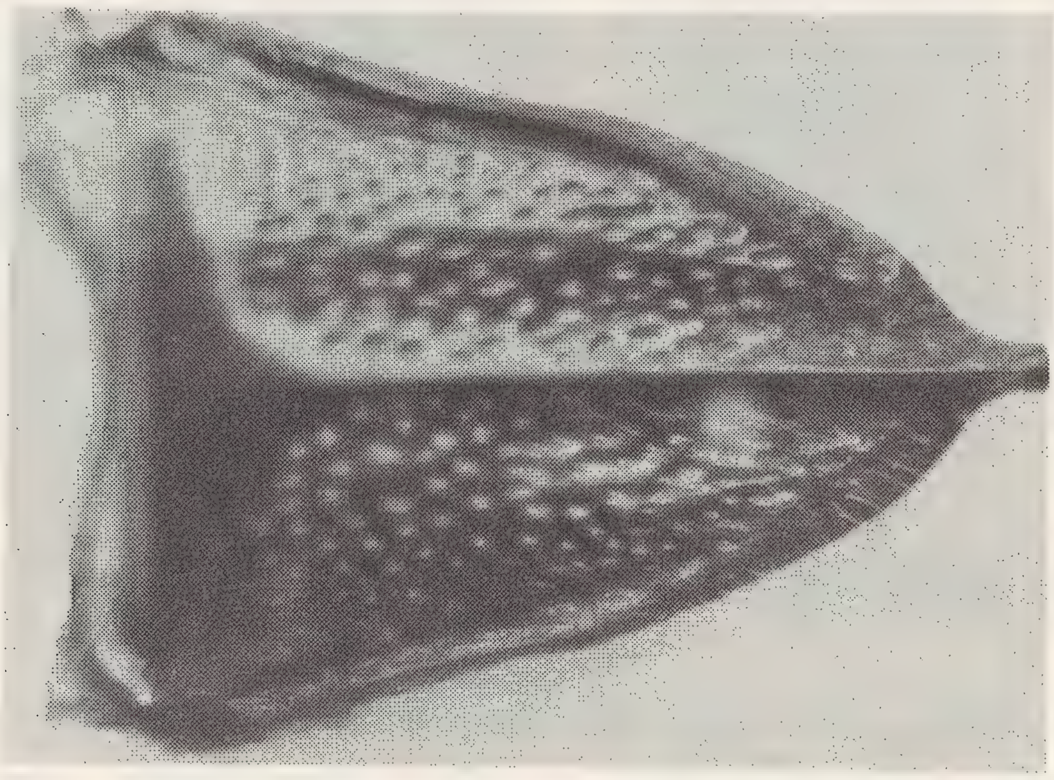


Fig. 2. Dorsal surface of the pygidium of an Agrilus granulatus liragus ♀ (X40).

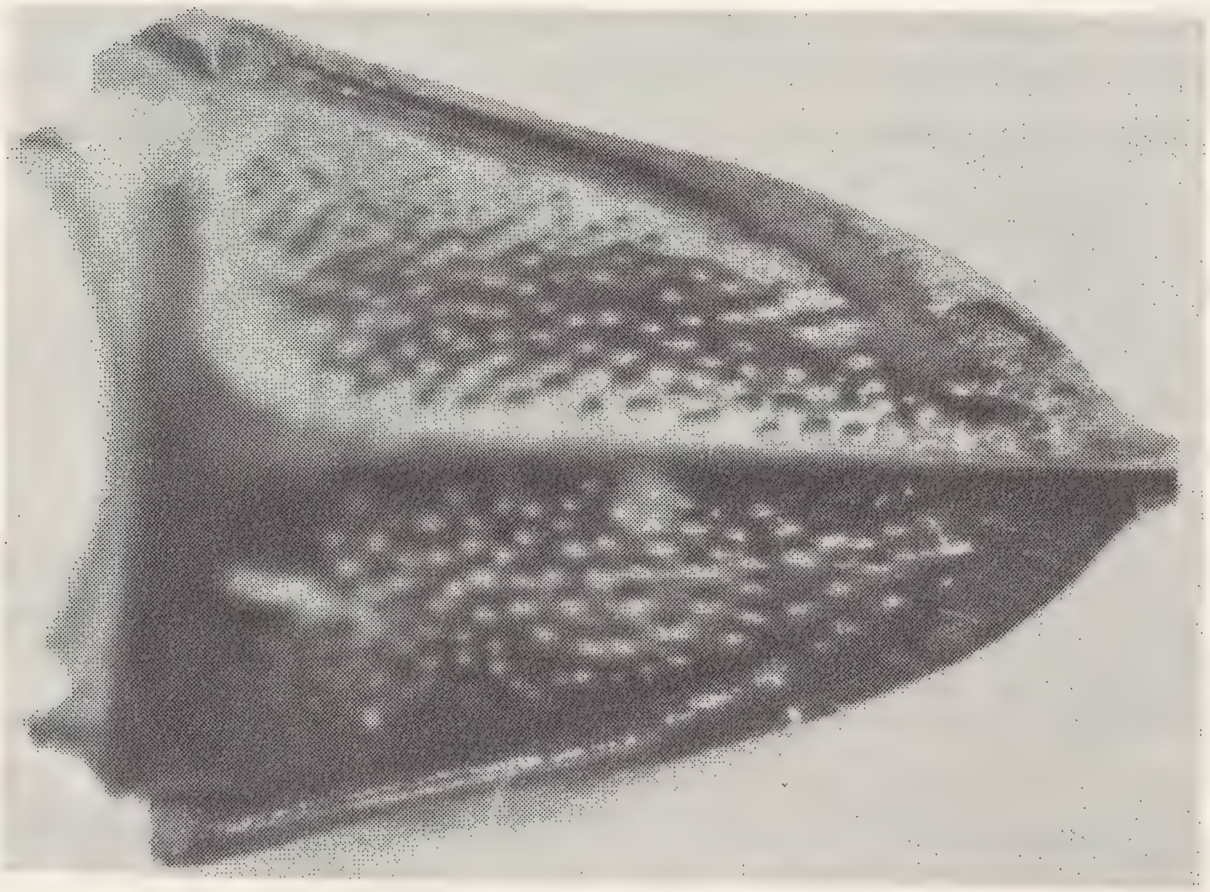


Fig. 3. Dorsal surface of the pygidium of an Agrilus anxius ♀ (X40).

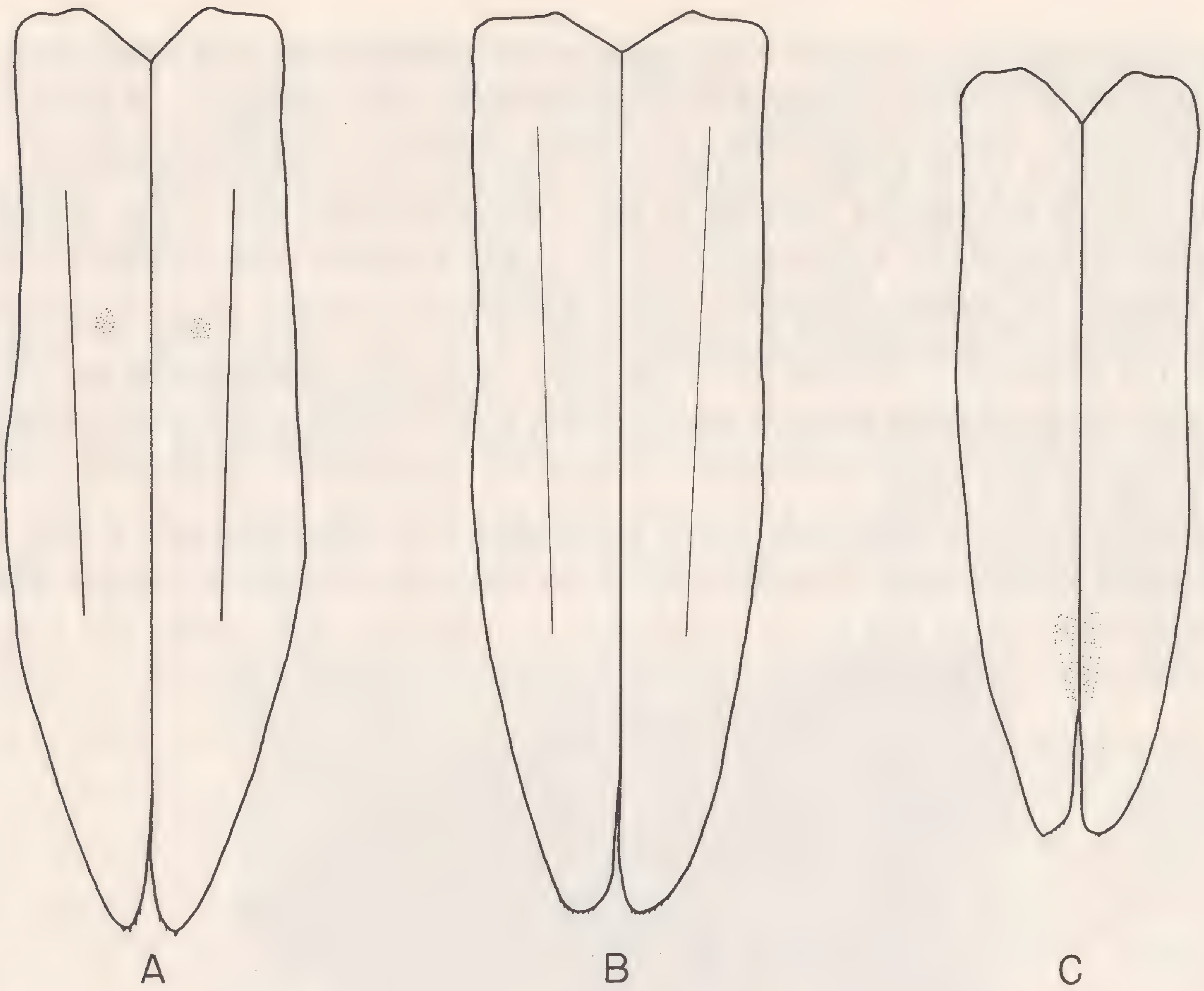


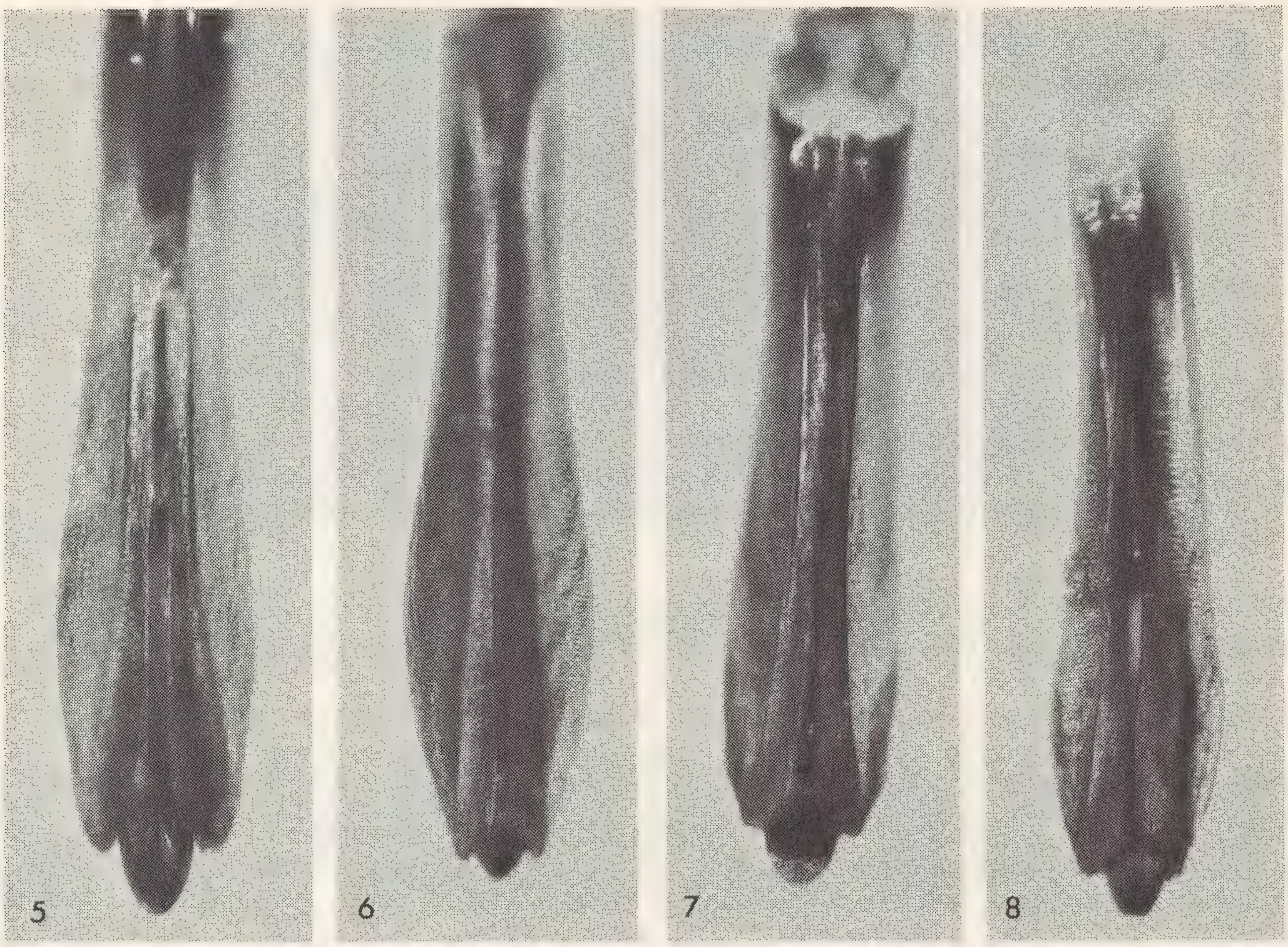
Fig. 4. Elytra of A. granulatus liragus ♂ (A), A. anxius ♀ (B), and A. pensus ♂ (C).

4a), while those of anxius are more broadly rounded and not as strongly toothed (fig. 4b). By using both the coloration differences and the somewhat obscure and somewhat variable structural differences of the pygidial spine, tarsal claws, and elytra it is usually possible to distinguish the females of anxius and g. liragus.

The most reliable characters for separating males of anxius and g. liragus are those of the aedeagus. The parameres of anxius have broad ventral inner margins, and these margins together form a trough which is broad and shallow (fig. 5). Ventrally, the inner margins of the g. liragus parameres are usually narrow, together forming a trough which is narrow but deep in comparison with that of anxius (fig. 6).

Nord et al. (1965) separate horni from anxius and g. liragus by utilizing characteristics of both the male and female genitalia. The ovipositor of horni (relative to elytron length) is significantly shorter than that of g. liragus or anxius. Nord et al. also pointed out that the average ovipositor length is less in g. liragus than in anxius, and in some cases the minimum length for g. liragus approaches the horni maximum. However, they found no overlap in ovipositor length between g. liragus and horni.

The male genitalia of these species correspond in length to those of the females. In addition to being shorter, the aedeagus of horni differs from those of anxius and g. liragus in having parameres which are less dialated posteriorally, their margins being subparallel (fig. 7). Nord et al. (1965) say that ventrally and subapically the inner margins of horni parameres are arcuate to subarcuate, while those of anxius and g. liragus are angulate to subangulate.



Figs. 5-8. Ventral sides of the aedeagi of *Agrilus anxius* (5), *A. granulatus liragus* (6), *A. horni* (7), and *A. pensus* (8).

The ventral trough formed by the parameres tends to be intermediate in form to the troughs of *anxius* and *g. liragus*, which are quite different from each other.

Despite the confusion which has occurred regarding the identity of *horni*, it is really quite distinct from either *anxius* or *g. liragus*. Besides the genitalic differences already noted, *horni* differs significantly from *anxius* and *g. liragus* in other ways. Most significant of all, perhaps, is the moderately dense pubescence on the marginal sclerites of the abdomen. As Horn (1891) points out, this pubescence appears all the more distinct because of the white pruinosity which is associated with it. Together, the pruninosity and white pubescence tend to form a white band which is very distinct on newly-collected *horni* specimens, but also quite noticeable on material that has been preserved for many years. The pubescence is usually dense enough to obscure the sculpturing of all the marginal sclerites, except for the last one. These marginal sclerites are usually less pubescent in *anxius* and *g. liragus*, and the pubescence is usually not dense enough to obscure the sculpturing of the marginal sclerites. Moreover, the marginal sclerite of the second abdominal segment is either glabrous or noticeably less pubescent than those of the first and third segments in *anxius* and *g. liragus*.

There are also distinct differences in the structure of the elytra. The texture of *horni* elytra is very even, the disc being comparatively smooth, finely imbricate, and usually lacking a distinct longitudinal costa (fig. 9). The disc is usually more coarsely imbricate in *anxius* and *g. liragus*, and often has a

Fig. 9. *Agrilus horni* ♂.

longitudinal costa and a rather distinct depression just mesad of the costa and between the disc's basal third and apical half. Frequently in *g. liragus*, and sometimes also in *anxius* (see ♂, fig. 39), this depression is pruinose, the pruinosity forming a spot similar those on the elytra of *g. granulatus*, but less distinct. Upon close examination, the parts of the depression where the spot tends to form can usually be seen to have a small group of recumbent hairs which are alingned differently and sometimes longer than the surrounding ones. The pruinosity usually disappears in preserved specimens, but the faint spot formed by the unaligned hairs can often be detected.

The recumbent pubescence on the elytra of *horni* is distributed rather evenly over the surface and is also rather short and uniform in length. That of *anxius* and *g. liragus* is usually not uniform in distribution or length, and many of the hairs are longer than those of *horni* elytra.

The structure of the head is also somewhat different in *horni*. The front is almost always rather flattened in profile. Sometimes in *anxius* and even less frequently in *g. liragus*, the front is somewhat flattened in profile, but in these species it usually bulges, presenting a rounded profile.

The form of *Agrilus pensus* is intermediate between that of *A. anxius* and *A. quadriguttatus* Gory, the latter being a willow feeding species. Barter and Brown (1949) say that the male genitalia of *pensus* are structured like those of *g. liragus* and *g. populi*, but this is not true. The *pensus* aedeagus (fig. 8) is somewhat variable, but more like that of *anxius* than that of *g. liragus* or *g. populi*. Barter and Brown also say that *pensus* lacks pubescent and pruinose spots on the elytra, but while they are not found on specimens from Nova Scotia and New Brunswick they are quite apparent on some specimens from Michigan and are also found on the type of the *pensus* synonym *betulae* Fisher. As in *A. quadriguttatus* and subspecies the subapical maculation of the elytra is likely to be spread out along the elytral suture instead of concentrated in a small spot. Also as in *A. quadriguttatus* the elytra are likely to be angulate at the apex (fig. 4c), forming a broad notch, instead of acuminate as in *A. granulatus* and subspecies, which have a narrower notch between the apices.

Eggs. The eggs of *pensus* (Engel, 1968), *anxius*, *g. liragus*, and *horni* are creamy white immediately after they are deposited. They are flattened and oval in outline. There seem to be no interspecific differences in egg size, those of *horni* being about 1.2 mm long by 0.8 mm wide, according to Nord (1962).

The eggs of *anxius* (and presumably *g. liragus*) are coated with a semi-transparent whitish substance immediately following deposition (Barter, 1957). The substance apparently acts as a cement and as a protectant for the soft egg shell. There is no evidence that *horni* applies such a substance to its eggs. Instead, the chorion of *horni* eggs appears to toughen as the larvae develop, and as a result they turn dark brown to black. The eggs of *anxius* and *g. liragus* darken like this only when parasitized. They develop grayish-black streaks and then become completely black prior to emergence of the parasite adult (cf Barter, 1957, 1965). This led Nord et al. (1965) to believe that the darkening of *horni* eggs may have been associated with parasitism, but this is not the case.

Larvae. Benoit (1965) presents a complete description of *g. liragus* larvae, and gives the differences between these and the larvae of *anxius*. He says the larvae of these species are about 30 to 40 mm long and 2 to 3.5 mm wide[1]. The body is white, except for the anal forceps and other minor sclerotized portions, which are ferruginous. The prothorax, which is wider than the rest of the body, has a median I-shaped sclerotized line on the tergum. A similar structure, which is only vaguely sclerotized, is located on the prosternum (Barter, 1957). The segments posterior to the prothorax are all about equal in width.

Benoit (1965) says C-shaped spiracles are located on abdominal segments one through eight, and similar, but somewhat larger ones are found dorsolaterally on the mesothorax. Actually, the sclerotized C-shaped structure is part of the spiracular valve, and the spiracular opening itself is located internal to the transparent valve.

Benoit (1965) states that the labial palpi are absent, but this is not true. Apparently he missed them because they were out of focus when his microscope was focused on the rest of labium (cf fig. 10 and his fig. 1B).

Because of the nature of his samples, Benoit's morphologic comparison of the larvae of *anxius* and *g. liragus* is of questionable value. He obtained his material from two localities, one for each species. This could hardly give one an adequate sample of intraspecific variation.

Nevertheless, the species differences in the coloration of the anal forceps which Benoit has listed do appear to hold for larvae collected in Michigan as well as for those from Quebec. The anal forceps of *anxius* are described by Benoit (1965) as being reddish, with the line of sclerotization extending anteriorally beyond the anal opening. He says the forceps of *g. liragus* are more brownish, with the sclerotization ending abruptly just posterior to the anal opening. The larvae of *pensus* and *horni* tend to be intermediate to those of *anxius* and *g. liragus* in both the structure and coloration of the anal forceps.

The characters Benoit (1965) used were worked out by Alexseev (1960). Among them was the location of a short macro-seta ("un pied petite") located in relation to a small circular depression or dimple in the cuticle. The dim-

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[1] Benoit (1965) does not specify the developmental stage of the larvae from which his measurements were taken.

Fig. 10. Labium of Agrilus granulatus liragus larva (X234). Note that the right palp is completely out of focus as with both in fig. 1B of Benoit (1965).

ples which are supposed to be associated with the pedalis structuralis (thoracic leg rudiments) are not evident on living larvae, and do not seem to be present with any regularity on specimens fixed in "XAAD" or by boiling. Consequently, the dimple may be the result of shrinking or swelling of the cuticle or associated tissues which may be related to the method of fixation and preservation. Benoit (1965) killed and preserved his larvae in 70 percent alcohol. There also seems to be the possibility that the absence of the depressions may have been related to the stage of larval development. Most of the larvae we examined had assumed the bent-over position in the pupal chamber. Benoit failed to mention the developmental state of the larvae he examined.

Benoit (1965) says there are also other marked differences between the larvae of anxius and g. liragus. As these require higher magnifications or more preparation, we did not examine Michigan material for these characters.

Pupae. There is nothing particularly unusual about the pupae of these species. All are creamy-white at first, and gradually assume the adult coloration. The eyes are the first parts to darken, and the elytra darken last. It appears to be during the period of pupal development that much of the adult structural variation arises, and it may very well be as much due to variation in the conditions under which the pupae develop as it is to genotypic variation.

GENERAL BIOLOGIES OF AGRILUS ANXIUS,
A. PENSUS, A. HORNI, AND
A. GRANULATUS LIRAGUS

Hosts and Ranges

THE BRONZE BIRCH BORER. A. anxius appears to be host specific to birches, Betula spp. Fisher (1928) lists the following birches as hosts for anxius: yellow birch, Betula lutea; paper birch, B. papyrifera; European white birch, *B. alba* (and varieties); gray birch, *B. populifolia*; and sweet birch, *B. lenta*. Barter and Brown (1949) also list *B. fontinalis* as a host for *anxius*. Hitchcock, et al. (1964) rank this birch as a variety of the western paper birch, *B. occidentalis*, which is closely allied to *B. papyrifera*. Harlow and Harrar (1958), in fact, call the western paper birch *B. papyrifera* var. *commutata*.

Although it has been reared from numerous hosts, the principal hosts for *anxius* are the native paper birches, *B. papyrifera* and *B. occidentalis*. *A. anxius* is, then, primarily confined to northern forest types, but its range extends somewhat south of the range of *B. papyrifera* in the eastern U. S., where it is found even at low altitudes as far south as Washington, D. C. It ranges west to Oregon and British Columbia.

THE BRONZE POPLAR BORER. *A. granulatus liragus* has been reared from several *Populus* species, although its principal host is trembling aspen, *Populus tremuloides*. In addition, Barter (1965) lists the following as hosts for *g. liragus*: bigtooth aspen, *P. grandidentata*; eastern cottonwood, *P. deltoides*; balsam poplar, *P. balsamifera* ssp. *balsamifera*; and the black cottonwood, *P. balsamifera* ssp. *trichocarpa* (Torr. & Gray) Brayshaw (1965).

The known range of *g. liragus* is very similar to that of *anxius*, but *g. liragus* does not occur as far south as *anxius* does in the eastern U. S. The southern edge of the *g. liragus* range seems to comply more closely with the range of *P. tremuloides* than that of *anxius* does with the range of *B. papyrifera*. Just how far north either *g. liragus* or *anxius* occur is not known, but both have been taken as far north as Edmonton, Alberta. The former, at least, should occur in interior Alaska.

THE ASPEN ROOT GIRDLER. Trembling aspen is the principal *horni* host, but bigtooth aspen and balsam poplar are also infested. Infestation levels on balsam poplar are sometimes quite high.

When seed stock of various species of poplars are transplanted in experimental orchard-like plots, *horni* can be particularly troublesome. Nord et al. (1965) found that under these conditions, *horni* readily infests the Eurasian species *Populus alba* and *P. tremula*. He found that various hybrid aspens were also infested. In nature, however, *horni* is probably confined mostly to species which reproduce by root suckering (i. e. aspens and balsam poplars).

Although *horni* has not yet been found as far west as *g. liragus*, it is probably not because the former has a more limited distribution, but is more likely a reflection of the fact that *horni* is not collected as readily as is *g. liragus*. There are specimens in the U. S. National Museum from Massachusetts to Arizona, and as far north as Aweme, Manitoba.

THE ALDER-BIRCH BORER. *A. pensus* has been reared from *Alnus rugosa* and collected on the foliage of this shrub. It has also been found in abundance on the foliage of green alder, *Alnus crispa* according to Barter and Brown, (1949). Fisher (1928) described *betulae*, a synonym of *pensus*, from specimens reared from river birch (*Betula nigra*) and Knull (1930) reared a large series from that host. The records of Blanchard (1889) for *Agrilus granulatus* collected on alders refer to *pensus*[1], not to *quadriguttatus* as Fisher (1928) suggests. Records for *pensus* on *Ostrya virginiana* are of questionable significance. One specimen collected by C. A. Frost (Monmouth, Maine; June 23, 1910) is labeled ''ironwood'' and three by Geo. M. Greene (Philadelphia,

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[1] Horn (1891) described *pensus* from the series taken by Blanchard (1889).

Pennsylvania; May 24, 1900) are labeled "hophornbean."[1] Not only is it rather doubtful that pensus infests Ostrya, but it is entirely possible that alders or young birches were mistaken for Ostrya. Ironwood, at least, is an unlikely host because its ecology is so very different from that of alders and river birch. A. pensus has been collected as far west as Aweme, in southern Manitoba, and in the East occurs as far north as mid-New Brunswick (Barter and Brown, 1949). Manee (1913) recorded Agrilus granulatus on "black alder" at Southern Pines, North Carolina. As it was collected with Eupristocerus cogitans Weber (an agriline species that infests alders), the record should be considered to refer to Agrilus pensus.

Life Cycles

A. anxius and A. granulatus liragus have a two-year life cycle under some conditions, but a one-year life cycle when other conditions prevail. A. horni and A. pensus, however, seem to have obligatory two-year life cycles.

ANXIUS AND G. LIRAGUS. When the eggs of anxius and g. liragus are deposited on hosts that are dying, severely injured trees or blowdowns, for example, the larvae often construct the pupal chamber during the same season that the eggs were laid. On the other hand, when oviposition occurs on more vigorous hosts, a two year life cycle results (Balch and Prebble, 1940; Anderson, 1942; Barter, 1957, 1965). Nonetheless, the larvae of these species cannot survive in healthy trees, and successful larval development is always dependent upon the host being in a weakened condition because of drought, repeated unsuccessful borer attacks, or other injuries (Barter, 1957, 1965).

PENSUS. The habits of A. pensus have not been studied sufficiently to establish the usual condition of its host at the time of oviposition. We have never seen larval galleries that would indicate a life cycle of less than two years for pensus. Furthermore, the larvae appear to overwinter primarily in two stages. Mature larvae, of course, overwinter in the pupal chamber, and early instar larvae are found overwintering deep within the xylem. Blanchard (1889) says pensus "breeds in and frequents stems of partly dead alders, but does not appear on the foliage very much." Knull (1950) says it breeds in "unhealthy" river birches, but mentions nothing about the size of the trees infested. Fisher (1928) says the pupal cells are common in the stems of young river birches that have died, and we have similarly found that the adult emergence holes are common on dead alders. However, numerous speckled alders were examined for the presence of pensus larvae, and those which harbor immature larvae are invariably alive, and many of those infested with mature larvae or later stages have not succumbed completely. Because the larvae always seem to require more than one year to complete development, the adults probably never oviposit on hosts imminently near death.

Only one attempt was made to attract pensus with cut stems of alders. Although there was a pensus infestation in the area, none were attracted. Oviposition on such material would be detrimental for this species, because early death would be inevitable for the larvae. The bark of Alnus rugosa is so thin that the phloem would become moribund and dessicated much too quickly to

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[1] Specimens in U. S. National Museum, Washington, D. C.

permit larval development. However, it seems probable that even large, decisively injured or felled river birches are not attractive to *pensus*.

HORNI . Nord (1962) found no evidence of anything less than a two-year life cycle for *horni*, and those findings are supported by our observations. By examining suckers containing mature larvae it is often possible to establish when the first instar gallery was formed. First instar larvae feed in the phloem[1] while moving down the stem toward the root, but in no instance was a first instar gallery located in the phloem of suckers infested with mature larvae. When it was not obliterated by the larva when it re-entered the stem, the dark spot indicating the position of the first instar gallery was invariably found between the outer two rings of xylem.

Moreover, out of 60 larvae introduced into suckers of various sizes, 5 larvae completed their development during the second summer. One larva matured in the laboratory during the third summer, but no larvae matured during the first season.

Nord (1962) found that the total length of *horni* galleries varied between 40 and 90 inches. The maximum length of the galleries of *anxius* and *g. liragus* which mature in two years is about 52 inches. The galleries of *anxius* or *g. liragus* larvae completing their development in one year are usually less than half that long (cf Barter, 1957; Anderson, 1944). Thus the evidence is overwhelmingly against the occurrence of a one-year life cycle for *horni*. Two years are usually required for *horni* development to be completed, but occasionally it may take three years.

Developmental Patterns

HATCHING OF EGGS . Barter (1957, 1965) found that incubation of *anxius* and *g. liragus* eggs requires about two weeks. The same is true for *horni*, and is probably generally true of many *Agrilus*. When embryonic development is complete, the first larval instar bores out of the egg and into the bark of the host, leaving the egg shell packed with frass.

LARVAL FEEDING PERIOD . Although larval behavior differs among *Agrilus* species, certain generalities can be made. As with most Buprestidae, the larvae never bore exit holes for their frass, but instead pack it tightly into the gallery behind them.

Heering (1956) gives a very detailed account of the larval behavior of *Agrilus viridis*. Some aspects of its behavior seem very similar to those of *anxius* or *g. liragus*, and other aspects seem typical for *Agrilus* in general. The *viridis* larvae are pressed tightly into the gallery. According to Heering this allows the microscopic spinules on the lateral muscular ridges to grip the sides of the gallery. The larvae move forward by constricting and stretching the segments telescopically. Movement of the parts of the body besides the head and anal forceps is entirely restricted by the sides of the gallery.

All the tissues macerated by the larvae pass through the digestive tract. As the frass passes out the anus, it is clasped between the anal forceps. With these the larvae pack the frass tightly into the gallery behind them (Heering,

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[1] Nord et al. (1965) said that during the first stadium the larvae feed in the cortex, but this is the position of the gallery one year after it is formed.

1956). It would seem necessary that the frass be packed at least enough to make its density as great as that of the tissues on which the larvae feed.

The Bronze Birch and Bronze Poplar Borers. Barter (1957, 1965) says that after they bore out of the egg, the larvae move directly through the bark to the cambial[1] region, but Anderson (1944) found that some larvae bore as much as 10 inches in the bark while passing obliquely to the cambial region. These species mine chiefly in the phloem, but the xylem is also scored. Anderson (1944) found that after reaching the cambial region, the larvae feed for an average of 1.3, 3.9, 7.1, and 13.0 inches in each of the four larval stadia preceding the molt to the fifth instar, after which the pupal chamber is formed. This indicates that there is a correlation between larval size and the amount of feeding done in any stadium. In the trees from which Anderson accumulated these data the points at which molting occurred were marked by departures of the gallery into the xylem. In hosts of a very decadent nature the larvae usually do not bore into the xylem before molting. On the other hand, in the more vigorous hosts which can be successfully infested, there are likely to be more xylem departures than molts. Apparently, these xylem departures are elicited by the unfavorable conditions occurring when host vigor is comparatively high.

Host condition also has a bearing on other aspects of gallery formation. In severely weakened or very decadent hosts larval galleries usually show no distinct pattern. Under these conditions, the larvae follow a course suggesting that they feed on the freshest phloem they encounter (Barter, 1957). These galleries can be fairly straight, but they usually meander without any pattern in these kinds of hosts.

In more vigorous hosts a zig-zag or sinuate gallery pattern is the rule. Under these conditions anxius makes a gallery which progresses in the direction tended by the phloem sieve elements or the xylem vessels, but weaves back and forth across their grain forming a gallery with continually expanding hyberbolic links (figs. 11, 16). Under similar conditions the successive links

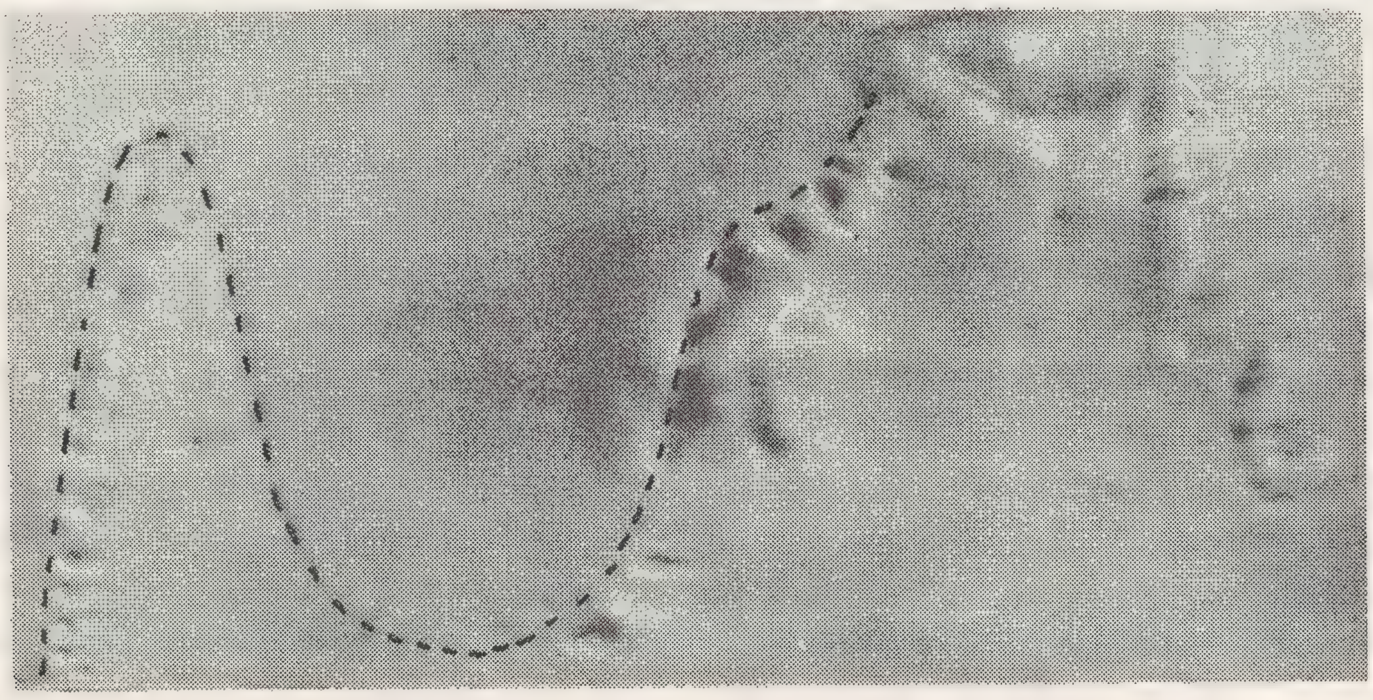

Fig. 11. Larval gallery of Agrilus anxius (in Betula papyrifera) that has healed over, indicating that it was made under conditions of high host resistance (from Anderson, 1944).

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[1] Some authors suggest that these insects bore in the cambium. The cambium is extremely thin (strictly defined, a single cell thick; cf Esau, 1953) and, therefore, it is inaccurate to say that these insects bore in the cambium. Although the cambium may be consumed as an insignificant part of the nutriment, food value is more likely to be derived from its derivatives, particularly the phloem and perhaps the newly-formed xylem.

of the g. liragus gallery are much closer together, often lying adjacent to each other (fig. 12). The attempt to explain these gallery patterns will be deferred to the part of this section which deals with host resistance.

The Alder-Birch Borer. The larvae of A. pensus boring in the stems of Alnus rugosa often form galleries without any regular pattern. Sometimes, however, the gallery is sinuate like those of anxius, particularly those parts of the pensus gallery which do not lie deeply in the wood. Xylem departures are more frequent with pensus larvae, and sometimes they bore through the wood from one side of the stem to the other, a behavioral trait noted by Barter (1957) for anxius when it bores in branches.

According to Larsen (1901) anxius larvae make spiral galleries in branches. This has never been reported for g. liragus, and pensus does not form spiral galleries, even when it bores in alder branches only about an inch in diameter.

Only one case was encountered in which several pensus larvae had completely girdled the phloem[1], and this was only during the latter stages of larval development. Very little is known about the larval behavior of this species, but it seems clear that if the host dies during the earlier stages of larval development, they would be unable to complete their development (cf page 16). Perhaps for this reason, mass attack is not the habit of this insect.

The Aspen Root Girdler. Some aspects of A. horni development seem to differ radically from what is characteristic of anxius, pensus, and g. liragus. In horni and often in the others, eclosion from the egg is followed by direct entry into the phloem, but the first instar gallery is otherwise quite different in horni. The mechanism triggering the first molt of horni larvae appears to

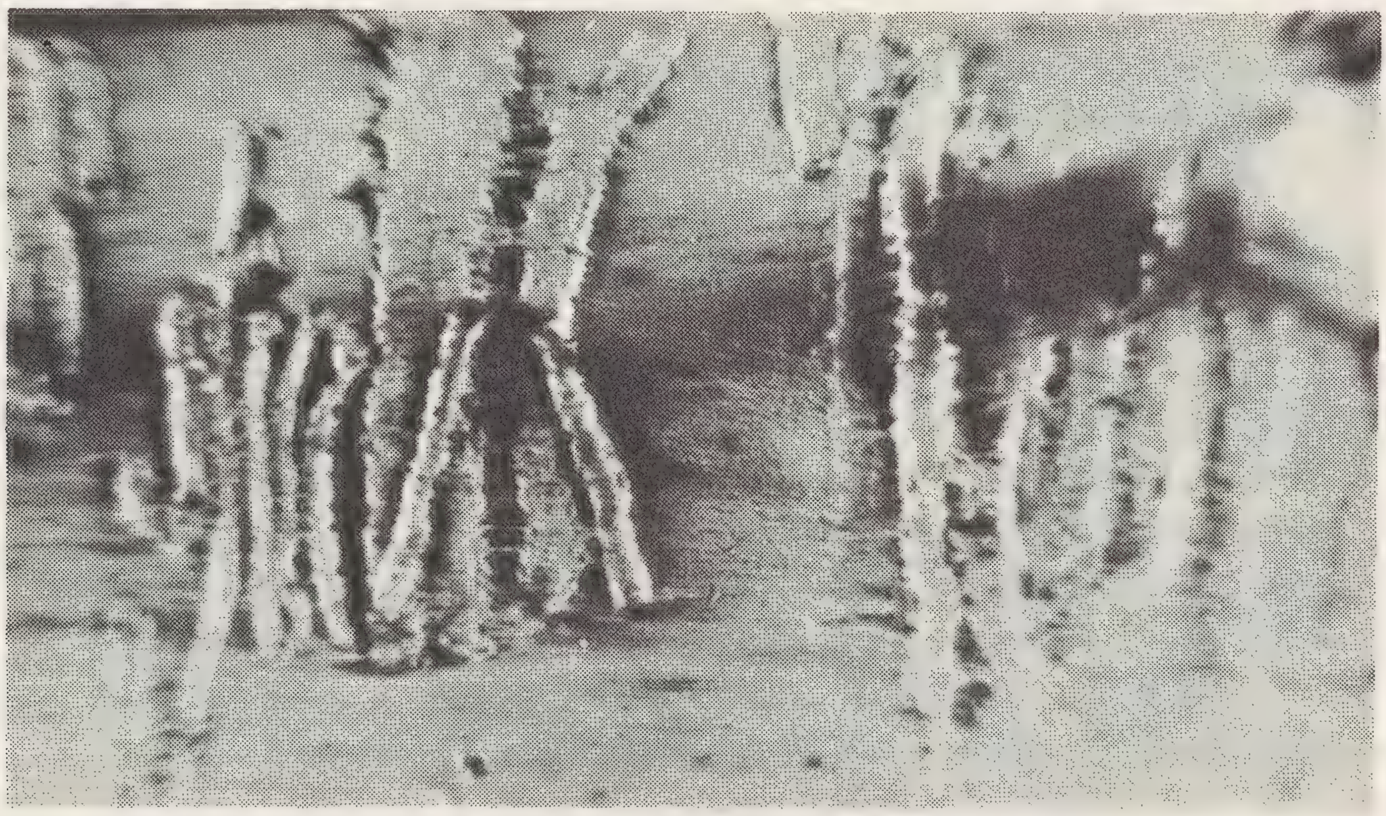

Fig. 12. Larval galleries of Agrilus granulatus (from area of intergradation of the nominate subspecies with g. liragus [see p. 85], but typical for the latter, at least). Some had healed over, indicating high host resistance (courtesy of R. E. Stevenson, Forest Biologist, Canada Dept. For. & Rural Dev., Calgary, Alberta).

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[1] Complete girdling may be more prevalent under some conditions than others. At Mallard Creek in Iron Co., Michigan, a moderately large pensus population build-up occurred one or two years after a stand of alders had been flooded by a beaver dam. In this area, alders that had been completely girdled by pensus were not rare (personal communication, 1968; R. P. Engel, University of Michigan, Ann Arbor).

be different, because the first instar galleries of this species are comparatively long. Prior to molting the first instar larvae of *anxius* and *g. liragus* bore an average of 1.3 inches after entering the phloem, although the gallery sometimes extends as much as 10 inches in the bark before it reaches the phloem (Anderson, 1944). In suckers recently killed by *horni* what appears to be the first instar gallery may extend out into a root for as much as 42 inches, and the total length of the first instar gallery usually is greater than 12 inches. Whether or not the first molt of the *horni* larvae occurs during the first season of development is unknown. No larvae have been found at this stage during the winter or spring. Presumably, they have been overlooked because of their small size (about 2 mm long in the first stadium).

Brooks (1914), presents an excellent discussion of the larval behavior of *Agrilus vittaticollis* Randall, which probably is a distant relative of *horni* (see fig. 44). He says that upon leaving the egg, the *vittaticollis* larva bores in the ''cambium'' (meaning cambial region) progressing down the trunk and into the root for a distance of 6 to 12 inches before boring into solid wood. For most of its length the gallery in the phloem is straight, generally following the grain of the wood. However, it sometimes zig-zags across the grain after leaving the egg, and invariably spirals once or twice in the phloem of the root before entering the xylem.

The larvae of *horni* behave similarly, but proceed with the grain until they enter the root. Just after reaching the root they are apt to make one or two spirals in the phloem, and often make others before they begin boring principally in the xylem. This behavior varies and may be dependent upon the size of the root and the condition of the host.

Sometimes the *horni* larvae do not bore in the xylem until they turn back toward the stem. In other instances they spiral in the xylem while still progressing away from the stem. Root diameter seems to be the factor determining where the larvae change the feeding direction. The turn is apparently elicited when the larvae reach a point where the diameter of the root they occupy is so small that they completely destroy the xylem. In aspens this is apt to occur where the root diameter is about 1/8 to 3/16 of an inch in diameter. The larvae may derive the stimulus eliciting the turn toward the stem when severing of the xylem results in different pressures on each side of the breach. While transpiration should make the pressure on the proximal side negative, any pressure in the distal part should be positive.

The turning point may be as much as 42 inches or more from the stem, but if the roots are short the larva may reverse its feeding direction only 6 inches from the stem. Instances in which the turning point is close to the stem are rare because the roots of aspen suckers are usually rather long.

The phloem in the roots of young aspen suckers is much thinner than that in aspen or birch stems suitable for infestation by *g. liragus* and *anxius*, respectively. The difference relates to the age-dependent accruement of inactive phloem. Although *horni* galleries lie principally within the xylem, it could hardly be otherwise. It appears that they consume the phloem too, and of all they ingest, the phloem probably provides most of what is assimilated.

After *horni* larvae re-enter the stem they sometimes bore a rather loosely spiralled or almost straight gallery which departs from the cambial region. Nord (1962), however, notes that the larvae always tunnel in the cambial region long enough to girdle the phloem. The root damage inflicted by *horni* larvae rarely seems to cause the death of suckers, because foliar discoloration occurs after the larvae return to the stem. Zahner and Debyle (1962) found that pruning only one half of the parent root of aspen suckers causes little mortality, even after two years. Consequently, *horni*-induced sucker mortality must be considered to result mostly from girdling of the stem.

The extent to which *horni* larvae feed in the cambial region after returning to the stem may be related to sucker vigor (Nord, 1962). Stager (1923) found that *Agrilus auricalceus* Redtenbacher (= *rubicola communis* Obenberger) boring in bramble (*Rubus* spp.) stems increases or decreases the distance between spirals such that the stem does not die until the period of pupal maturity. Apparently, the death of the stem is a crucial factor, because Stäger says the pupae require a dry chamber. This seems to be true for species in the *anxius* group, as well. One might, therefore, expect variations in the position of *horni* pupal chambers to be at least partially related to moisture conditions in the stem at the time of its construction. Their pupal chambers are located an average of 4.8 inches above ground, but the position varies from a height of 2 inches to 14 inches. (Nord et al., 1965).

POST-FEEDING LARVAL PERIOD

Formation of the Pupal Chamber. Brooks (1914) made a detailed analysis of pupal chamber formation by *A. vittaticollis*. The *vittaticollis* larvae extend a burrow of the usual dimensions through to the bark at the upper end of the gallery. They then recede about 1/4 inch and begin eating wood from the sides of the gallery. As this proceeds, their feeding is directed backward along the ventral side of the body, thereby doubling the gallery diameter. The two ends of the body are, as a consequence, appressed closely together, and the head and anus soon lie side by side at the bottom of the pupal chamber. The chamber is then complete, but the larvae continue to move forward until the head and anus are at its upper end.

The larvae of all *Agrilus* spp. probably construct the pupal chamber similarly. However, when the layers of birch bark are gradually peeled off over *anxius* pupal chambers, a small loop in the gallery is found at the upper end of the chamber (exit point for imago). The loop apparently marks the point at which the larva turned in the bark and re-entered the xylem. It appears to be peculiar to *anxius*, and may somehow relate to the peculiarities of birch bark. The loop is not evident at the exit points constructed by *g. liragus* larvae, and *horni* and *pensus*, at least, must double back in the manner Brooks (1914) has observed for *vittaticollis*.

Shortening of the larva may be initiated earlier in most of the other species of the *anxius* group than it is in *vittaticollis*. Whereas *vittaticollis* initially settles in the pupal chamber with the body folded in half, the larvae of other species assume a position in which the body is folded between the second and third abdominal segments. While *vittaticollis* has both head and anus at the upper end of the chamber, the other species have the folded portion of the body at the upper end, the anus at the lower end, and the head pointed downward adjacent to the abdomen (in standing trees). This would indicate that instead of stopping where *vittaticollis* does, with head and anus at the upper end of the gallery, they move around farther. An alternative possibility is that after boring to the outer layers of bark, they merely turn back and feed along the ventral side of the body until the gallery width is doubled, then gradually recede or shrink to the overwintering position. This seems unlikely, however, as the exit point is plugged with frass. Unless these *Agrilus* have acquired the ability to pack frass with the mouth parts and head, it must be assumed that the anus, at some time, is at the upper end of the pupal chamber. Brooks

(1914) implies that it is the fourth instar vittaticollis larva which constructs the pupal chamber, which may explain the difference in the folding position for the abdomen in this species. The molt to the fifth instar occurs before formation of the pupal chamber in pensus, anxius, horni, and g. liragus, and the fifth instar larvae are noticeably shorter and more stout than fourth instar larvae.

Diapause. Barter (1947) has shown that it is necessary for anxius larvae to reach the fifth instar before overwintering in order for pupation to occur the following spring. He says that subjection of fifth instar larva in the pupal chamber to subfreezing temperatures is necessary for the continuation of development.

In early October 1966, some sections of a small birch tree infested with anxius were collected near Manistee, Michigan, and stored indoors with the intention of removing the larvae from them at leisure. In November part of them were debarked, and none of the larvae had shrunk to the prepupal form. In early December, however, adults emerged from these logs, and a few more issued in late December. Some larvae, on the other hand, did not enter the prepupal stage, suggesting that only some of them had been exposed to low temperatures in the proper stage and for a sufficient duration before they were brought indoors. This is in agreement with recent theories which, according to Wigglesworth (1964), suggest that diapause involves some phase of development that can proceed only at low temperatures.

While the transition from the overwintering stage to the prepupal stage may be possible only after some exposure to low temperatures, the transition itself appears to occur only when temperatures are above freezing, and probably considerably higher. In Michigan the transition of anxius, g. liragus, and horni larvae to the prepupal stage occurs during the spring. In Benzie Co., the transition of liragus larvae, in some cases, occurs before late April, but usually is later. In Iron Co. some horni larvae do not go into the prepupal stage until early June.

PUPAL TRANSITION. In Iron Co. the transition from the prepupa to the pupa usually occurs in May and early June for anxius, g. liragus, and horni. There is no delay in development when the pupal stage is reached, and soon after the all-white pupa forms it begins to take on some of the adult coloration. The eyes are the first parts to darken, and the mandibles darken next (Barter, 1957). The elytra remain white until most of the other parts of the body have darkened, and do not come to rest in the adult position until rather late in pupal development. Very likely, this is the reason that the wings are deformed more frequently than other parts in rearing these beetles. When drying of the wood around the pupal chamber is too rapid, the elytra may not take shape properly, after uncurling from the sides of the abdomen. This usually results in a poor fit of the elytra along the suture, causing a gap which exposes the membraneous wings. Sometimes the deformities are more extreme.

ADULT EMERGENCE

Study Procedure. Eclosion of the adults from the pupal chamber was followed in several ways. Unfortunately, no good field emergence data were obtained for g. liragus, and no attempts were made to get records of field emergence for pensus.

In 1964 g. liragus emergence began about May 30, which was considerably earlier than was expected. Consequently, there was not sufficient time to locate enough pupal chambers for checking field emergence adequately. Some data were obtained by placing small triangular screen cages (fig. 13) over the exit points that were exposed by cutting away the outer bark layers. The same method was employed in 1965, but because emergence was considerably delayed the results were extremely poor. Dessication of the exposed bark layers and wood prior to the beginning of the emergence period caused high mortality of the pupae and young adults.

The same type of cage worked well for analyzing field emergence of anxius. To expose the exit points for anxius adults, only a few outer layers of birch bark had to be removed. Consequently, the rate of dessication of inner bark and wood probably differed insignificantly from that of infested trees not treated in this way. A. anxius emerged normally from caged trees in 1964 and 1965. In 1964 the cages were checked intermittently, only often enough to roughly establish the beginning, end and peak period of emergence. In 1965 they were checked daily, except on days when emergence was unlikely.

In 1964 the emergence of horni adults was followed in the field by examining some infested suckers marked with flagging. Although the plot was checked only every other day, this method proved to be rather inefficient. Hence, different methods were used in 1965. The basal portions (sticks) of 123 infested P. tremuloides stems were placed in a clearing at the University of Michigan Forestry Camp near Beechwood, where they received full sunlight during the middle of the day. The ends of the sticks were waxed, and the pupal chambers were then located by comparing the sticks with their X-ray[1] negatives. Tubes of plastic screening were positioned over the segments of the sticks harboring the pupal chambers, and the ends of the tubes were constricted by stapling or taping. The sticks were held in an upright position near the ground by cords strung between stakes (fig. 14). They were checked daily.

It is probably safe to say that in most parts of their ranges, peak emergence for anxius, g. liragus, and horni occurs during June, but even within a given region there can be significant year-to-year variations in the emergence pattern. The variations in emergence periods relate to weather variations. Davis and Raghuvir (1964) compared deviations from long term mean air temperatures with emergence data for A. aurichalceus. The temperature data used were those for the month of March, April, and May. Walton (1951)

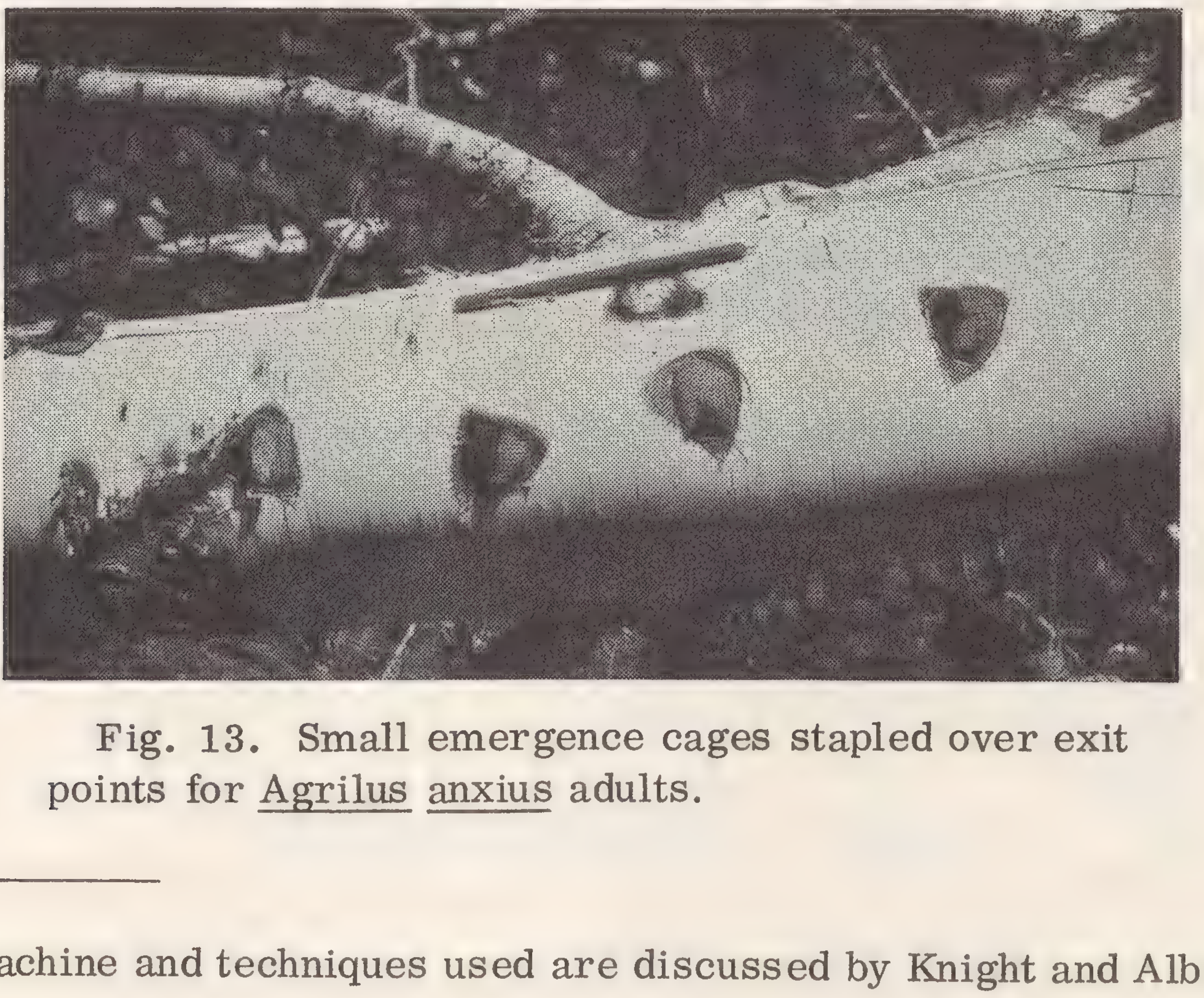

Fig. 13. Small emergence cages stapled over exit points for Agrilus anxius adults.

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[1] The X-ray machine and techniques used are discussed by Knight and Albertin (1966).

Fig. 14. Plot at Camp Filibert Roth near Beechwood, Michigan, where the emergence of Agrilus horni was studied under semi-natural conditions by stringing the infested sticks between stakes to hold them vertically.

employed the same technique for studying the emergence of A. ruficollis Fabricius for successive years. Emergence appears to be sufficiently well correlated with monthly temperature data to make the technique useful.

Results and Discussion. Table 1 shows the deviations from long term monthly means for Stambaugh, Michigan for March, April and May in 1964 and 1965 (U. S. Weather Bureau, 1964). The average deviation for 1964 was +0.97 degrees, while that for 1965 was -1.23 degrees. Emergence data for these two years reflect the differences.

In 1964 anxius emergence began in the Stambaugh vicinity about June 4 but not until June 14 in 1965. The difference between peak emergence times was even greater, being about June 7 or 9 in 1964, and between June 20 and 23 in 1965. In 1964 horni emergence began about June 7, but was delayed until about June 20 in 1965. Peak emergence was between June 9 and June 15 in 1964, while it occurred between June 21 and June 28 in 1965 (fig. 15).

The 1964 emergence periods of horni and anxius did not extend past the end of June, but in 1965 both species continued emerging into July. Surprisingly, one anxius adult was found alive in an emergence cage on August 4, but with this unusual exception, emergence of this species ended by July 7. A. horni emergence ended on July 15, making the duration of the 1965 emergence period about equal to that for 1964.

Table 1. Average deviation from long-term mean air temperature (F) for Stambaugh, Michigan.

Month	Year	
	1964	1965
March	-2.2	-5.6
April	+1.3	-2.1
May	+3.8	+4.0
Mean	+0.97	-1.23

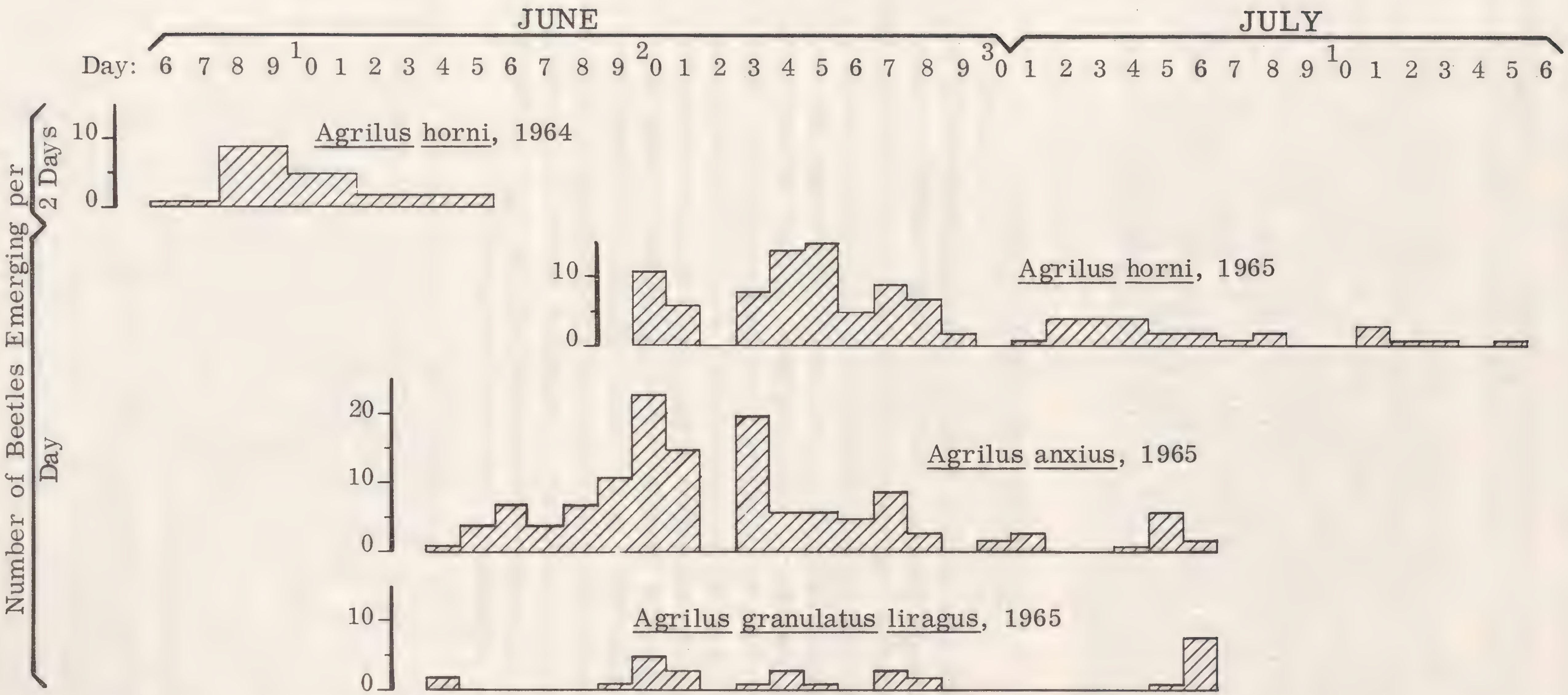

Fig. 15. Adult emergence dates of Agrilus spp. in Iron Co., Michigan. Note the following: (1) Five horni emergences occurred from the 16th through the 29 th of June, 1964; for this interval the plot could not be checked and specific emergence dates are unknown. (2) One anxius adult was found alive in an emergence cage on August 4 and would have been dead if it had emerged more than 1 or 2 days before.

Barter (1949) found that the mean emergence dates for *g. liragus* preceded those for *anxius* by an average of 12.7 days. Although data obtained for *g. liragus* in our study were rather poor, it is evident that the differences in time of emergence are not as great in Michigan. *A. g. liragus* began emerging about 7 or 8 days before *anxius* in 1964, but the peak emergence periods were not as far apart.

Anderson (1944) reared both *anxius* and *g. liragus* from caged aspen and birch logs in Minnesota. He considered the possibility that he was working with two "host races," so one might assume that he would have noticed any significant difference in emergence times. In combining the emergence data for both *anxius* and *g. liragus*, Anderson found that emergence began on May 29 and ended on July 2, the peak occurring on June 10.

A difference in peak emergence times for *g. liragus* and *anxius* would appear to have no more real significance than any other differences between these species, and may be subject to the same kinds of geographic variation. These beetles are, in any case, actively mating and laying eggs during time spans which are nearly coextensive.

Population Regulating Factors

The factors which are usually considered important in the regulation of insect populations are parasites, predators, and weather conditions. There have been many semantic arguments devoted to the question of whether or not factors which cannot take an increasing toll on an organism as its density increases can be as important as factors that can increase their toll with density. Because factors like weather conditions have no way of responding to density, it is usually assumed that they fall in the former category. More often than not, though, weather conditions are clearly a part of the climatic scheme to which a species becomes adapted. There may be some variations of weather which occur so infrequently that they are not likely to bring about genetic adaptation in the species affected. Such catastrophic factors are here considered to be of secondary importance as population regulating factors; a species must, in the long run, be part of a density dependent controlling system. The factors likely to be of major importance in controlling the *Agrilus* being considered here, are parasites, predators, and host resistance.

HOST CONDITION. Host resistance can be regarded as an indirect effect of weather conditions, but it is probably more valid to consider it to be a manifestation of the more or less balanced relationship between the host and its phytophagous parasite, and a manifestation of the physiological condition of the host. The physiological condition of trees is most directly related to their age and site quality. By loosely applying these two variables one could explain most of the interactions which occur between *Agrilus* spp. and their hosts but the balance of the interrelationship is also influenced by parasites and predators, both phytophagous and entomophagous.

The Bronze Birch and Bronze Poplar Borers. Anderson (1944) says the larvae of *anxius* or *g. liragus* require living "cambium" if they are to complete their development successfully. Inner bark tissues which have died and turned brown are unsuitable for larval development. Barter (1957) found that some first instar *anxius* larvae may bore 13 to 18 inches without molting in moribund phloem. Those that are able to molt bore about twice as far (6 inches) as larvae feeding in phloem which has not turned brown. The evidence seems to indicate that these larvae require nutrients associated with living phloem and that these essential nutrients decompose when the phloem cells die.

Swaine (1918) and Balch and Prebble (1940) reported finding *anxius* attacking and killing many healthy, mature birches in Canadian forests. Nash et al. (1951) reported that during times of high bronze birch borer population levels, healthy trees are attacked and killed. Different opinions were held by Spaulding and MacAloney (1931) and Hall (1933), who believed that the borer attacks birches because they are “dying.”Barter (1957) suggests that the borer may appear to be more aggressive under outbreak conditions, but that it otherwise plays only a secondary role. He and Anderson (1944) present evidence showing that the beetles are usually unable to successfully attack healthy trees unless they are exposed to repeated unsuccessful borer attacks in successive years. Of course, after such repeated attacks, the trees could not be considered healthy, and persistent attacks of this sort could only occur during extended outbreaks. Perhaps unsuccessful attacks indicate that the number of susceptible trees is limited, or that “spill-over” occurs from highly attractive trees onto less attractive ones adjacent.

It is apparently only when many trees are simultaneously predisposed to infestation that the bronze birch borer becomes epidemic. *A. granulatus liragus* apparently does not often reach the outbreak state, but Barter (1965) and Barter and Cameron (1955) found that following repeated defoliation by the forest tent caterpillar, *Malacosoma disstria* Hber., aspens are predisposed to *g. liragus* infestation. Under such conditions *g. liragus* can cause deterioration and death of hosts it attacks either on branches or the main stem. Arru (1962) discusses the factors which predispose newly transplanted poplars in northern Italy to attacks of *Agrilus suvorovi* Obenberger (=*viridis populnea* Schaeffer). Problems with this insect arose only after poplars were planted on soils which were not as well suited to them as the deep friable soils to which poplar cultures were formerly confined. Arru believes that the factors which make the transplants susceptible to infestation by the beetle are those preventing resumption of growth following planting. The most important of them is moisture stress, which is likely to occur when poplars are transplanted on sandy or pebbly soils, on embankments, or in compact, poorly aerated soil.

Anderson (1944) treated aspens and birches in a number of ways to determine the severity of injury, if any, necessary to predispose them to the attacks of *g. liragus* and *anxius*[1]. He made some interesting observations on brood development in 6 aspens and 6 birches which were girdled in September, 1940. All of these trees, except one of the aspens, remained alive throughout the summer of 1941, when they became infested with *g. liragus* and *anxius*. Brood density below the girdles in the aspens averaged 1.2 per sq ft (52 sq ft examined), while above the girdles there were only 0.1 larvae per sq ft (88 sq ft examined). Similar results were obtained for the birches. Below the girdles all the living borers were either pupae or adults, but only larvae were found above the girdles during the spring of 1942.

All of the trees produced a small annual ring above the girdle during the summer that they were attacked by *Agrilus*. No growth rings were produced below the girdles in any of these trees, however.

When Anderson (1944) debarked the girdled trees he found that the bark

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[1] Both taxa were still lumped under the name *anxius* at that time.

moisture content below the girdles was nearly 2 times that above. He assumed this to be a reflection of conditions that had existed during the previous summer. This assumption is incorrect because girdling trees by cutting through the phloem causes starvation and death of the roots. After the roots of a girdled tree die, water absorption ceases and the rest of the tree probably dies slowly from dessication (Kramer and Kozlowski, 1960). Because the phloem above the girdle continues to receive small amounts of carbohydrates, while that below gets none, the former should maintain a higher moisture content. It is the presence of solutes (sugars, etc.) in the phloem which allows its turgidity to be maintained. The diffusion pressure deficit of phloem sap offsets the effects of negative pressure or tension in the xylem. Therefore, the high bark moisture contents Anderson found below the girdles in the spring of 1942 were possible only because the bark had absorbed moisture during the winter. Hence, he has used a false premise in asserting that the larval mortality in trees with a proliferating cambium is not related to bark moisture content.

Heering (1956) found a relationship between bark moisture content and the susceptibility of beeches (Fagus sylvatica) to attack by Agrilus viridis. However, he claims that in some cases callose formation becomes the important host resistance factor, especially in trees so extensively dessicated that defensive sap flow is impossible. Because callose is a polysaccharide consisting of linked glucose units (Kessler, 1958), its formation involves a process much like normal growth. The growth of trees is probably controlled more by water availability than by any other environmental factor (Kozlowski, 1964), and deficits in water availability can cause physiological conditions which override growth regulatory processes (Zahner and Donnelly, 1967). It is, therefore, difficult to see how severely dessicated trees could form callose fast enough to pinch off continuously feeding larvae. The most logical explanation is that when Heering thought larval mortality was attributable to callose formation, the larvae had, in fact, been overwhelmed by phloem exudates, and were afterward being overgrown by callose. Even his own observations support this contention. He found that in very moist, vigorous bark, the virdis larvae construct vent holes ("Rindensaft-Abflusskanalen") which prevent sap from accumulating in the gallery by allowing it to drain off to the outside. The very fact that the larvae have time enough to cease forward movement and push the anterior part of the body through the bark, suggests that wound callose formation could not be rapid enough to kill them.

Heering (1956) found that the moisture content of bark infested with first instar larvae is almost as high as that of sound bark. This could indicate that bark which appears to be sound may really have low vigor, or instead, that his technique is too crude for measuring the essential differences between susceptible bark and bark resistant to infestation. He removed his bark samples from the trees, placed them in glasers' putty, and analyzed their moisture content in the laboratory. His index of tree resistance was bark moisture content expressed as a percentage of its total dry weight. This measure of host resistance is not precise because the active phloem constitutes a very small fraction of the total bark mass. Critical differences in its turgidity would be masked by variations in other bark factors, such as the amount of accumulated cork or innactive phloem. Perhaps a refinement of the technique, such as that used by Bier (1964) would give better results.

However, phloem pressure would probably be a better measure of active phloem borer resistance for the majority of woody angiosperms. Some of the angiosperms have gum ducts and may have resistance mechanisms analogous to those of conifers. For some conifers a close relationship between oleoresin exudation pressure and tree resistance to scolytid attack has been demonstrated (see for example, Vité, 1961). While the nature of conifer oleoresin ducts and their products makes pressure measurements relatively easy, host resistance could not be studied as readily for species whose chief resistance mechanism is the exudation of phloem sap. Piercing the phloem causes an injury which interferes with its normal activity. However, the observations of Heering (1956) suggest that useful pressure measurements might be obtained without tapping the active phloem itself. He says that even before the heads of newly-hatched *Agrilus viridis* larvae have completely entered the bark, they are often repelled by exuding sap which detaches the egg shell from the bark. Without the shell to push against the larvae are helpless.

If, as it appears, phloem pressure is actually the most important host resistance factor encountered by phloem feeding *Agrilus* it should follow that the serpentine galleries, like those often produced by *g. liragus* and *anxius* are an adaptation giving them some advantage for withstanding the copious flow of sap. In starting a zig-zag or sinuate gallery pattern, a larva makes an initial cross-grain segment, then turns abruptly and reverses its direction. When it begins to bore past the lateral extent of the gallery segment to which it is adjacent, the larva usually reverses its direction.

Heering (1956) believed that the sinuate galleries produced by *Agrilus viridis* larvae are the consequence of a fixed pattern of behavior, although they do not follow a sinuate course in very decadent hosts. Barter (1965), on the other hand, found that *g. liragus* makes galleries with very close transverse segments in relatively vigorous hosts, while in more decadent ones the gallery becomes more sinuous resembling those of *anxius*. Like xylem departures, which for *anxius* or *g. liragus* increase in number with increasing host vigor, the zig-zag or sinuate gallery pattern may be elicited as a sort of avoidance reaction.

There seems to be little reason for assuming that the effect of phloem sap on the larvae could be anything other than simple suffocation. Presumably, when the larvae make departures into the xylem, the plug of frass behind them protects them from the copious influx of phloem sap. The advantages which might be derived from a serpentine gallery pattern are more nebulous, however.

Barter (1957) suggested that by staying beneath the previously formed parts of the gallery, the larvae are protected from the downward, translocation of sap. However, downward progressing galleries do not seem to prevail over those progressing upward in standing trees. Barter (1957) knew that galleries can proceed in either direction, and his hypothesis is, therefore, inadequate, even for explaining the facts as he knew them.

Moreover, there seems to be good reason for believing that movement of sap in the phloem of even the most vigorous of trees which *Agrilus* can infest is, at most, very slight. Trees susceptible to *Agrilus* infestation are not healthy and, without exception, must be subject to high internal moisture stress. According to the mass-flow theory, phloem transport occurs from areas of higher osmotic sap concentration to regions of lower concentration. During the growing season, the direction of transport would normally be from the crown toward the roots. However, when trees are under severe moisture stress, the rate of respiration in the crown may equal or exceed that of gross photosynthesis. Under such conditions there may be no transport of carbohydrates in the phloem, and its turgidity must become significantly lower than in trees not under moisture stress.

Furthermore, serpentine or zig-zag galleries are produced even in logs, if they are infested rather soon after being cut. This is strong evidence suggesting that they are produced in response to local turgidity rather than to the mass flow accompanying the translocation of carbohydrates. It seems fairly apparent that even when moisture stress is too great for the translocation of carbohydrates to occur, the phloem is still sufficiently turgid for sap to infuse into sieve elements that have been severed. When Agrilus larvae cut through the sieve tubes, part of the exuding sap is probably absorbed by the inactive phloem and the xylem. Consequently, the pressure of sap in gallery should be lower than that in the surrounding phloem. In spite of the fact that successful infestation must invariably be attended by low turgidity in the phloem, sap should pass slowly from it until it loses its turgidity entirely or until its pressure comes into equilibrium with that in the gallery.

If the foregoing premises are valid, the function of the sinuate or zig-zag gallery pattern may be unrelated to phloem transport or to minimizing the amount of sap that enters the gallery. It seems possible that they minimize only the detrimental effects of sap oozing from newly-severed sieve elements, as is illustrated in figure 16. When a larva turns back adjacent to the priorformed gallery link, the phloem inside the turn is cut off between the links forming a peninsula. These peninsulas should not exude as much sap as the phloem outside the turn. The minimization of sap influx from the peninsula might make it possible for the larvae to minimize its suffocating effects by opening the spiracles on the side of the body adjacent to the peninsula. With each successive link, then, the larvae could open the spiracles on alternate

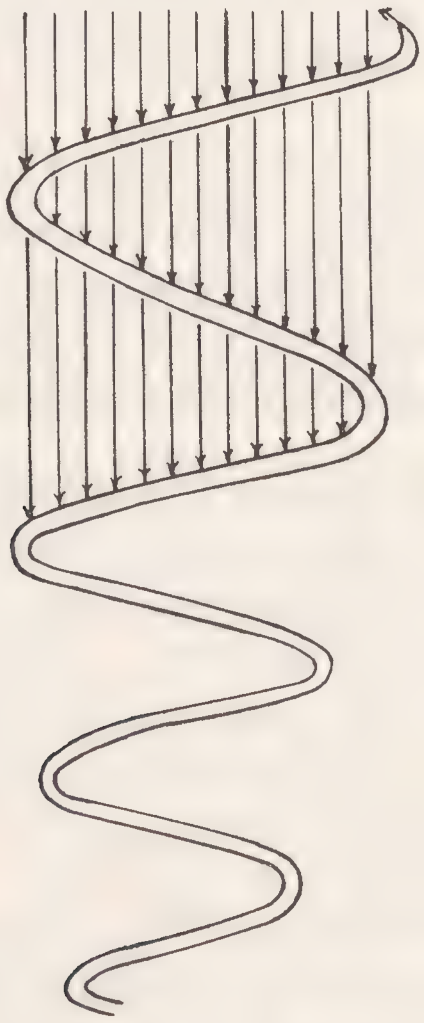

Fig. 16. Sinuate gallery pattern similar to that of Agrilus anxius. The vertical arrows indicate the hypothesized direction of sap infusion into the gallery after severing of the phloem sieve elements (no active transport is occurring). Because the body of the larva is appressed very tightly to the walls of the gallery, alternately opening the spiracles on the side of the body exposed to the smallest amount of sap infusion, might allow continual respiration.

sides of the body.

The differences in the pattern of the *g. liragus* and *anxius* galleries may be partially related to differences in the phloem structure of birches and poplars. It is not sound evolutionary thinking to assert that the gallery differences are attributable either to genetic differences in the insect species or purely to differences in the hosts. In other words, it is pointless to try to separate the combined phenotypic effects of environment and genotype.

A. anxius or *g. liragus* larvae in relatively vigorous hosts construct longer galleries than those living in weaker hosts. Barter (1957) found that *anxius* which matured in one season in rapidly dying birches, made galleries of only 15 to 20 inches, while those in more vigorous trees matured in two years, after boring 20 to 52 inches. Anderson (1944) gives similar data for *g. liragus* development. The reason for the vigor-related variations in gallery length are apparently unknown, but two possibilities are evident: (1) larvae feeding in relatively vigorous tissues perhaps must expend more energy in attaining the nutrients necessary for complete development, or (2) molting of late larval stadia may occur only under certain conditions, such as those relating to host physiology, time of year, or both. There are no published data from which it is possible to ascertain if the gallery segments for all larval stadia are longer in more vigorous hosts or if the increase in gallery length is built up during a particular portion of larval development.

The Alder-Birch Borer. Very little is known about the relationship between *Agrilus pensus* and its hosts, *Alnus* spp. and *Betula nigra*. Because it is often difficult to distinguish *pensus*-infested speckled alders (*Alnus rugosa*) from uninfested ones, it seem likely that *pensus* plays a more primary role in causing the death of these shrubs than do *g. liragus* and *anxius* in infesting their respective hosts.

It is very difficult to trace out complete *pensus* galleries because they meander extensively through the xylem and a number of galleries may intersect. Consequently, no attempts were made to accumulate data on total gallery length. It seems likely, though, that the average length of *pensus* galleries will approach the maximum length for *anxius* or *g. liragus* galleries. Because dying speckled alders are probably not suitable hosts for *pensus*, these insects are always contending with a level of host resistance which is found only in the more vigorous of the hosts suitable for *anxius* or *g. liragus*. Moreover, many speckled alders show signs of unsuccessful attacks, and successful ones do not seem to occur very frequently. Much of the earlier portion of larval life is spent in the xylem, and the mortality rate of young larvae seems to be very high.

Blanchard (1889) records one location in Massachusetts where he found *pensus* (under the name *granulatus*) in rather large numbers. Barter and Brown (1949) collected a large series of *pensus* on *Alnus crispa* var. *mollis* and suggest that it is particularly well-adapted to this alder, which is confined to the Atlantic seaboard. However, *A. c.* var. *mollis* does not appear to differ greatly in form or in habitat from *A. rugosa*. Furthermore, in June, 1968 an area in which *pensus* adults were moderately abundant was encountered at Mallard Creek in Iron Co., Michigan. The creek bottom was flooded by beavers during the previous summer and possibly also in the summer of 1966. It, therefore, appears that, at least throughout most of its range, *pensus* becomes numerous only infrequently, particularly because of the host resistance controlling factor.

The Aspen Root Girdler. *Agrilus horni* has different means for coping with host resistance than have anxius, liragus, or pensus. First of all, rather than attacking dead or dying hosts, it limits its attacks to those poplar suckers small enough to be overwhelmed, and those on which eggs are deposited appear to be of normal vigor. The vigor of aspen suckers must be affected by the root girdling of horni larvae. Zahner and Debyle (1965) found that pruning either of the parental roots of Populus grandidentata suckers about 4 or 5 years old usually causes a significant reduction in the growth of the suckers over a span of two growing seasons following treatment. Usually, horni larvae completely masticate the xylem in one of the roots in which they bore. This occurs at a point where the diameter of the root is about 1/8 to 3/16 of an inch in diameter, and its chief function may be to elicit the turn of the larva back toward the stem of the host (see page 20). However, because water absorption occurs mainly in a zone 1 to 10 cm from the apex of a root (Kozlowski, 1964), the xylem girdling may induce moisture stress or increase it in the stem of the host and in the part of the root proximal to the girdle. If the xylem girdle occurs in a branch of a main (or parental) root, or if it sometimes does not occur at all, the survival of larvae may depend upon their ability to effectively girdle the phloem, thereby causing starvation in the distal part of the root or preventing food from reaching the stem and proximal part of the root from the parent tree (ortet). There are probably definite size limits on roots which can be effectively girdled in either manner.

In 1960 Nord (1962) measured the diameters of 150 horni-killed suckers. He found that 84 percent of these had diameters of 0.5 inches or less. He was, however, unable to demonstrate that horni shows a preference for small suckers because a similar percentage of the suckers in the stand he sampled had diameters below 0.5 inches. Studying the same area in 1962, Fowler (1963) found that 71 percent of the infested suckers had diameters below 0.5 inches, while about 76 percent of the healthy ones were below that size. Using regression and variance analysis, he compared the relationship of sucker height to diameter for infested suckers with that for uninfested ones, and found no difference. His illustrations show the two sets of height-diameter data to be strikingly congruent.

Fowler (1963) lists the numbers of infested and uninfested suckers in each of the age classes from 1 to 6 years, and his data are presented in table 2.

Table 2. Age-class frequency distribution of healthy and Agrilus-killed Populus tremuloides suckers[a]

Age	Number of Suckers	
	Healthy	horni-Killed
1	0	1
2	3	13
3	19	58
4	55	51
5	53	23
6	20	4
Total	150	150

[a] Modified from Fowler (1963).

When the two distributions are made comparable by subtracting one year from the age of the healthy suckers, it can be seen that the age-class frequencies of infested and uninfested ones are very similar. It must be remembered that suckers which died at age X were actually selected by females at age X-1. Hence, the suckers available to horni females in this area were from 1 to 4 years old. The maximum height of suckers in the area would have been about 6.5 feet. This is near the maximum size of suckers on which horni eggs have been found.

The data of Nord (1962) and Fowler (1963) seem to indicate that the horni females were ovipositing randomly with respect to sucker size. It appears that when the eggs were laid, few of the suckers were too large to elicit oviposition, or that too few were sufficiently above the optimum size for survival of larvae to make it apparent in the statistics.

A small experiment was initiated in 1964 to examine the effects of host resistance on horni larvae. Four groups of 15 Populus tremuloides suckers were chosen with the intention of introducing first instar horni larvae at their bases. Two groups were composed of suckers beginning their second year of growth, and the other two groups of suckers were starting their fourth growing season. They will be referred to as 2-year-old and 4-year-old suckers.

An area was picked in which the likelihood of having the experiment confounded by natural infestation was low, although this approach, admittedly, has undesirabilities. A random sample of the heights of 2 and 4-year old suckers was taken. Heights were measured with a leveling rod and were recorded to within the nearest one-tenth foot of the point where the previous season's growth terminated.

The mean heights were calculated for each age class. Within each age group, height classes of ±1 standard deviation from the mean were set as the sizes for suckers to be chosen for the experiment. The resultant height values for 2-year suckers were 1.3 and 3.2 feet, while those for 4-year-old suckers were 3.7 and 7.4 feet. These treatments will be referred to as 2-year-, 2-year+, 4-year-, and 4-year+, respectively. On selecting the suckers for the experiment a ±0.2 foot leeway from the treatment value was allowed.

Eggs for rearing the horni larvae were procured from 10 cheesecloth cages which were placed over individual aspen suckers (fig. 17 and 18). A pair of beetles was introduced into each of the cages, and the eggs were collected periodically. The eggs were removed in groups by cutting away a portion of the bark on which they had been deposited. After the eggs were removed additional soil was placed in the can which enclosed the base of the suckers so that subsequent oviposition would occur on smooth, uninjured bark.

The eggs and bark to which they adhered were placed in small incubators, which consisted of 1 by 3 inch white pine blocks with five shallow depressions made with a 1/4 inch drill (fig. 19). The eggs were placed in the depressions and a microscope slide was fastened over the tops of the blocks with masking tape. To keep the incubators moist, dampened paper toweling stapled to wood strips was held in contact with the ends of the wood blocks by rubber bands. The pan in which the incubators were placed was covered to prevent dessication.

A camel hair brush was used for transferring larvae. They were placed in small petri dishes lined with moistened blotting paper and transferred to the test suckers as soon as possible. The larvae were placed in small cavities cut in the bark about one inch above the sucker bases. The cavities were

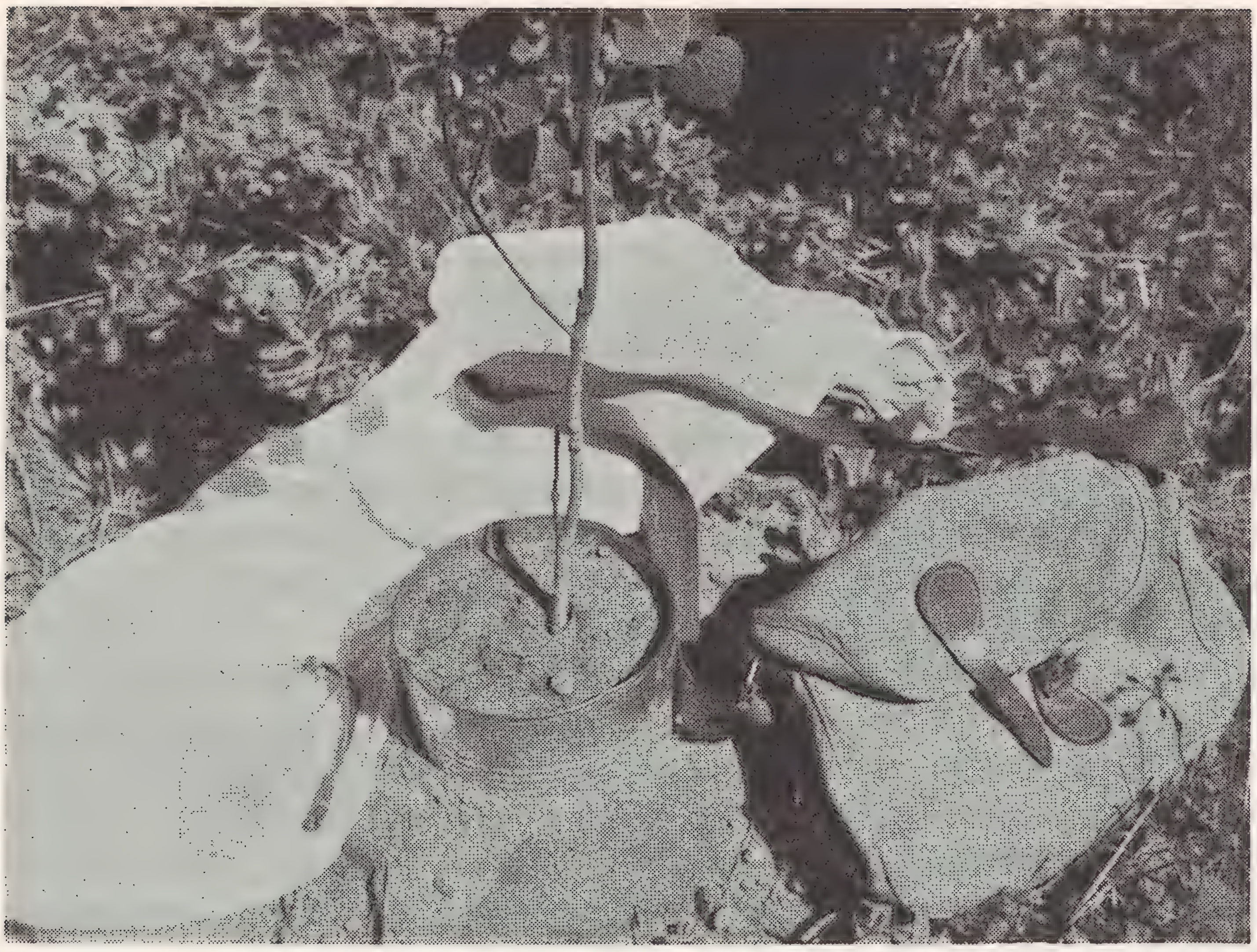

Fig. 17. Unassembled cheesecloth cage for Agrilus horni oviposition.

Fig. 18. Assembled cheesecloth cage for Agrilus horni oviposition.

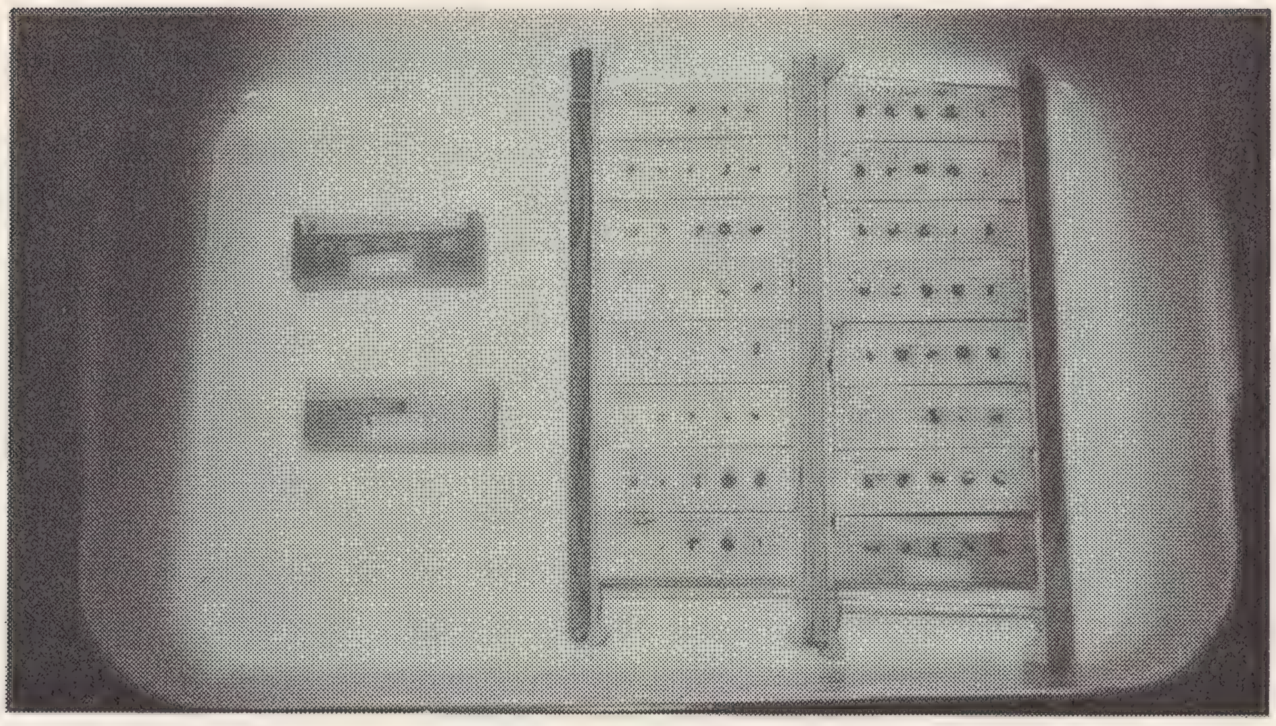

Fig. 19. Wooden incubators for Agrilus eggs. Standard microscope slides (1 X 3 inches) are taped over the tops to cover the small depressions holding the eggs.

prepared with a sharp scalpel by making two horizontal incisions about one eighth inch apart through the bark to the surface of the xylem. The incisions were cut obliquely downward so that when the strip of bark between them was pried out, the cavity formed would keep the wriggling larvae from falling out.

After the larvae were placed in the cavities, they were covered over with tape. Test suckers were subsequently revisited for checking on the survival of the larvae. Those which had died before boring into the exposed phloem region were replaced. All dead larvae were replaced until all suckers harbored larvae which had started into the phloem. It was necessary to replace seventeen larvae before all suckers were infested, although it was apparent when the suckers were examined in 1966 that some of the larvae probably died after boring a very short distance. Introductions were begun on July 25 and completed on July 31, 1964. A few days following completion of the introductions, the cavities in the bark were filled with grafting compound to prevent fungal infection or dessication at these points.

Evaluations were made by digging up the suckers and their roots on May 4 and 5, 1966. The larval galleries were traced by cutting into the stems and roots with a sharp knife. The results are tabulated in table 3. It can be seen that only one larva matured in a 2 year- sucker, and none completed development in the 4 year+ suckers. Six of the larvae which eventually formed pupal chambers were in the 2 year+ (2) and 4 year- (4) suckers.

The data are, of course, rather meager, but it is likely that survival in the 2 year- and 4 year+ treatment was poor primarily because of the unfavorable conditions for the larvae in the roots. In 6 of the 2 year- suckers the larvae had to bore in roots that were, perhaps, too small to allow successful development. Larvae are known to have successfully matured after spiraling over a span of only about 6 inches in small roots, but this is probably not always possible. Survival of horni larvae was probably impossible in three of the suckers having roots of adequate size, because the roots were diseased and decomposing at various points.

One of the 2 year- suckers had a very large root, about 1 1/2 inches in diameter. Such large roots probably are not suitable for horni larvae either,

Table 3. Development of *Agrilus horni* larvae in selected *Populus tremuloides* root suckers.

Treatment[a]	Number of Larvae		
	Boring at Least Short Gallery	Boring More Than 10 Inches	Completing Development
2yr-	14	8	1
2yr+	14	8	2
4yr-	11	5	4
4yr+	11	4	0
All	50	25	7

[a] Suckers were in their second (2yr) and fourth (4yr) growing seasons when larvae were introduced and had heights (±0.2 ft; see p. 33) of 1.3 ft (2yr-), 3.2 ft (2yr+), 3.7 ft (4yr-), and 7.4 ft (4yr+).

probably because they cannot be girdled readily. Large root size was undoubtedly an important factor contributing to mortality in 4 year+ suckers too, but some of the larvae in these suckers seem to have perished even before reaching the roots.

All the information so far assembled indicates that *horni* can kill healthy aspen suckers. However, there is an upper limit to the size of hosts it can subdue. It also seems likely that, if other factors are equivalent, the suckers on areas of good site quality are able to resist infestation better than those on poor sites. The areas in which *horni* is likely to establish persistent populations are ones where suckers spring up in fields at the edges of stands of larger aspens or in areas where the aspen clones do not expand rapidly to fill the intervening spaces. The site quality in such locations is usually low even in the former case, but is invariably poor in the latter. *A. horni* is usually not found in areas of high site quality, and never becomes abundant on such sites. Nevertheless, one should not assume that their scarcity in areas of high site quality is directly related to the poor survival of larvae in these areas. The *horni* adults seem to orient to open areas, and good sites usually produce dense, closed stands. Moreover, the adults may have evolved this affinity for open areas at least partly through the effects of genetic selection channelled via differential survival of the larvae.

Poor aspen sites which are left rather denuded after fire, like the main study area of Nord (1962) and Fowler (1963) are likely to be good *horni* habitats after the aspens have suckered. The numbers of *horni* in such places should decrease rapidly over a period of 6 to 8 years, however, In fact, in 1964, approximately four years following the year of peak abundance, there were only a few *horni*-infested suckers to be found on the plot where Nord and Fowler had worked. The largest infested suckers listed in their data had diameters of 1.0 inches (6 inches above base). *A. horni* eggs were not found on suckers larger than 0.9 inches at the base. It appears as though host selection may be the factor limiting the sizes of suckers which are actually infested. Again, the crucial survival factor would appear to be root size, and this certainly correlates rather well with stem size. Although host resistance may not directly limit the upper size of suckers in which *horni* larvae can live (i.e., by simply causing the mortality of those above the upper limit) one must presume that adult host selection behavior is evolutionarily directed by the ultimate results of it.

PREDATORS. Woodpeckers are the only predators known to exert any population limiting effect on *anxius* and *g. liragus*. Their predation on *g. liragus* is confined to standing trees (Barter, 1965), and the same is probably true for woodpecker predation on *anxius*. Knight (1958) found that the feeding of woodpeckers on bark beetles has the greatest effect when the beetle infestations are heavy and infested trees are concentrated. Similarly, Barter (1957) found that their predation an *anxius* appears to be more prevalent in heavily infested trees. One might then expect that the effectiveness of this predation would be rather variable depending upon the size and concentration of populations, although other factors are probably also important. Nash et al. (1951) found that the toll of woodpeckers on *anxius* varied from very slight in some areas to as high as 30 percent in others. Barter (1957, 1965), however, found that woodpeckers consumed as much as 50 percent of *anxius* brood, and removed up to 40 percent of the *g. liragus* brood from their pupal cells. Anderson (1944) says that about 10 percent of *anxius* and *g. liragus* prepupae were consumed by woodpeckers.

Woodpecker predation is confined to the spring, apparently occurring only after the larvae begin the transition to the prepupal stage. Barter (1957) believed that woodpeckers fed on *anxius* at that time only, but later (1965) he found that the pupae of *g. liragus* were consumed and presumed that adults were also eaten.

Woodpeckers are also an important population limiting factor for *pensus*. It appears that the predation on *pensus* occurs during the winter. Large numbers of *pensus* brood are never found in a single *Alnus rugosa* stem, but the extent of concentration of infested alders may affect woodpecker activity. It seems that once a woodpecker finds the first *pensus* pupal chamber in a stem he is likely to find them all, although there usually are not more than 7 or 8 in a single stem.

We have seen spiders and ants attacking the adults of *g. liragus* and *anxius*, but they probably cause little mortality. These beetles usually apress the legs to the thorax and fall free of the host in time to avoid being caught. In one instance, however, an ant had grasped its falling prey and both predator and prey fell to the ground where they couldn't be found. The quickness with which these beetles take flight or drop to the ground, especially on hot days, is apparently reflected in Gory's name *anxius* (*nomen nudum* of Dejean), and it seems rather unique that *torpidus* Leconte has been placed as a synonym of the former.

Nord et al. (1965) observed ants mouthing the eggs of *horni* on caged aspen suckers. Since ants frequently pass up and down the stems of suckers, often in visits to sources of aphid honey dew, they may encounter the *horni* eggs which are placed above ground level. Because many eggs survive to hatch, they do not appear to be particularly attractive to ants, however.

PARASITES. Nash et al. (1951) listed eight parasite species which were reared in cages containing logs infested with *anxius*. It is certain that some of the Ichneumonidae they list as *anxius* parasites were instead reared from other insects[1]. *Glypta* sp. and *Pimplopterus* sp. are parasites of Lepidoptera, while

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[1] Identifications made for Nash et al. were undoubtedly reliable as they say these were made by Townes and Muesebeck, both prominent specialists.

Olesicampe sp. is a sawfly parasite. None of these could have been reared from anxius.

The parasite Barter (1957) reared from birches was identified for him as Ephialtes sp., but has more recently been identified as Dolichomitus messor perlongus Cresson[1]. The Ephialtes species reared from Populus by Barter (1965) is probably the same species. The parasite identified for Nash et al. (1951) as Ichneumon sp. is probably Dolichomitus sp., perhaps D. messor perlongus. Nomenclatural corrections in the usage of Ephialtes Schrank and Ichneumon L. have reinstated their application to groups parasitic on Lepidoptera[2].

Townes and Townes (1960) record D. messor perlongus as being reared from Saperda calcarata Say, and S. concolor Leconte, and it also parasitizes Oberea shaumii Leconte. Townes[3] expresses doubt that females of messor perlongus could develop on Agrilus spp.

The records of several braconids reared by Nash et al. (1951) from anxius are probably legitimate. The species are Atanycolus charus Riley, Spathius simillimus Ashmead, and Doryctes atripes Provancher. They also reared the chalcid, Phasgonophora sulcata Westwood.

Barter (1957) reared an additional braconid from anxius, Helconidea ligator Say, but did not rear Doryctes. However, he records Doryctes sp. parasitizing g. liragus (Barter, 1965). Besides the Ephialtes sp. already discussed, other parasites Barter reared from g. liragus were Atanycolus charus, Phasgonophora sulcata, and the eulophid, Tetrastichus sp., listed as probably being near rugglesi Rowher.

Barter (1957) says that Atanycolus and Phasgonophora were the most important larval parasites of anxius, parasitizing 1 to 52 percent (average 14 percent) and 1 to 8 percent (average 4 percent) of the larvae, respectively. Other parasites were recovered only occassionally. He recovered parasites from only 9 percent of all larvae in his samples. Therefore it appears that total parasitism was not usually as great as is indicated by the percentages listed above, which were calculated for a sample of 600 larvae.

The only parasites which was consistently reared from g. liragus larvae by Barter (1965) is Phasgonophora sulcata, which parasitized from 2 to 20 percent of the larvae. Other parasites were reared less frequently.

Parasitism on larvae of anxius and g. liragus may amount to a rather insignificant portion of the total mortality factors which regulate their populations. The same cannot be said for egg parasitism, however. Barter (1957, 1965) and Nash et al. (1951) found that parasitism was consistently high on eggs of anxius and g. liragus, usually being near 50 percent for both species. Apparently, two chalcidoids were about equally important, even though in in-

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[1] The specimens reared from Betula were lent to us by Mr. Barter for identification, but those he reared from Populus has been accidentally destroyed.

[2] The revision of the Ephialtinae by Townes and Townes (1960) had led to the change for Ephialtes, and Ichneumon, sensu Townes (1944), included Dolichomitus, sensu Townes (1960).

[3] Personal communication, 1966; H. K. Townes, American Entomological Institute, Ann Arbor, Michigan.

dividual cases the species were alternately dominant. One was identified as *Thysanus* sp. (Thysanidae) and the other is an encyrtid near *Coccidencyrtus*.

While the egg parasites of *anxius* and *g. liragus* must be more important in population regulation than the parasites of the larvae and pupae, the reverse seems to hold for *horni*. Only four eggs in a sample of 147 (about 3 percent) taken in 1965 were found to be parasitized. The parasite was identified as *Oobius* sp.[1]

Although they are exposed to parasites for a shorter time than the larvae of *g. liragus* or *anxius*, *horni* larvae are parasitized much more heavily. *A. horni* pupae are also parasitized rather frequently. Total parasitism of larvae and pupae was about 42 percent in 847 rearings, with *Tetrastichus nordi* Burks being reared most often. This eulophid is quite small and probably lays its eggs on the larvae when they spiral just beneath the bark in the stem, between the time of their emergence from the root and formation of the pupal chamber. This was deduced from observing the behavior of a few *T. nordi* females in the laboratory and from X-ray pictures of *T. nordi* larvae developing just beneath the bark on larvae that never formed a pupal chamber. Usually, however, the *horni* larvae are not killed by *Tetrastichus* until after the pupal chamber is formed.

Emergence of *T. nordi* adults corresponds with the time when *horni* larvae are re-entering the sucker stems (August and early September). An average of 49.1± 17.1 adults emerged in a sample of 49 broods. The size of the adults and their sex ratio is quite variable.

Three ichneumonids were found with about equal frequency in *horni* pupal chambers. They parasitized a combined average of approximately 13 percent of the *horni* collected. These parasites have longer ovipositors, enabling them to place eggs on the larvae and pupae within their pupal chambers. *Xylophrurus agrili* Viereck has been reared from *horni* larvae and pupae in both spring and fall. Brooks (1914) says this species has two generations per year. He found it to be an important parasite of *A. vittaticollis*, which bores in the roots of various trees and shrubs of the family Roseaceae. In the fall it lays its eggs on the *vitaticollis* larvae at about the time they are forming the pupal chamber. The spring brood attacks pupae or larvae just prior to pupation. *A. vittaticollis* may be the primary host for *X. agrili*, as Brooks found it to destroy from 25 to 40 percent of the larvae and pupae of this beetle.

Xylophrurus bicolor maurus Townes emerged from *horni* pupal cells only during the spring, and all of the collecting and rearing records which Townes and Townes (1962) list for *X. bicolor* indicate that the adults fly only during the spring. *X. bicolor* seems to have a diapause similar to that of many *Agrilus* spp., requiring an extended period of cold for development to be completed. It is perhaps for this reason that efforts to rear the adults from suckers collected during the initial stages of larval development are not very successful.

No rearing records were previously available for *X. bicolor maurus*. However, the western subspecies, *X. bicolor bicolor* has been reared from an insect in *Salix* sp. and from *Saperda moesta* Leconte infesting *Populus balsamifera* ssp. *trichocarpa* (Townes and Townes, 1960).

The third ichneumonid, *Mastrus smithii* Packard, was incapable of emerging from *horni* pupal cells. The only adults obtained were removed from the infested suckers where they died, often after boring only part of an exit hole.

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[1] Determined by B. D. Burks, U. S. Dept. Agr., A.R.S., Entomology Res. Div., Washington, D. C.

The mandibular teeth of these specimens are usually worn considerably. This species is known to be a secondary parasite on the ichneumon fly Gambrus extrematus Cresson and has been reared from the coccoons of two sawfly species (Townes, 1951). It seems likely that it is poorly adapted for emerging from Agrilus pupal cells, and probably parasitizes ichneumonid parasites of other insects with greater success, particularly those in the coccoons of cecropia moths.

Besides Tetrastichus nordi, several other Chalcidoidea[1] were reared from horni pupal chambers. They caused about 6 percent mortality of the horni reared in this study, and this was attributed principally to Lampoterma sp.[2], a pteromalid. This parasite emerges about mid-May, and therefore, oviposits chiefly on prepupae or pupae of horni. From 3 to 10 adults develop in each horni pupal chamber. This Lampoterma sp. appears to be limited to one generation per year by an obligatory pupal diapause.

Eurytoma magdalidus Ashmead (Eurytomidae) was reared from several horni pupal cells, but this species may be a secondary parasite. In two instances it is known to have emerged from pupal chambers which harbored two different types of parasite larvae.

Some of the larvae and pupae which died for unknown reasons (17.7 percent) may have been killed by parasite stings. Consequently, the impact of parasitism may be underestimated.

ADULT BEHAVIOR

Feeding and Maturation

Barter (1957) found that Agrilus anxius females, maintained in the laboratory, fed about 6 days before showing any tendency to lay eggs. Adults of anxius and g. liragus are not found mating or ovipositing in the field until about 2 weeks following emergence. There is no reason to suspect that the same is not true for horni and pensus.

Oghushi (1963) found that under laboratory conditions Agrilus auriventris auriventris Saunders females formed ova 5 to 6 days after emergence, but full grown ova were not present until 8 to 10 days after emergence. Oviposition began on or after the eleventh day following adult eclosion. Ogushi found no full-grown ovaries in females which had not fed. Their development was very slow in unfed beetles, many of which did not live long enough to reach the oviposition stage.

Similar developmental requirements are probably common to most, if not all, Agrilus. Some unfed anxius females dissected quite soon after emergence had partially developed ova. Without food, however, these females are probably unable to form fully-developed eggs, and usually die after a rather short time.

A. anxius adults were maintained successfully during the winter on pieces

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[1] Determined by B. D. Burks, U. S. Dept. Agr., A.R.S., Entomology Res. Div., Washington, D. C.

[2] Nord et al. (1965) list this species as Metastenus sp., but the application of Metastenus has recently been changed (cf Burks, 1967).

of apple, but in nature their feeding is, no doubt, restricted to leaves. Hutchings (1923a) says the bronze birch borer feeds more readily on the foliage of poplars and willows than on birch. Barter (1957) found that *anxius* adults consume the leaves of poplars, particularly those of *Populus tremuloides*, more readily than those of *Betula papyrifera*. The findings of Nash et al. (1951) differ slightly; in their laboratory studies *anxius* showed the greatest preference for *P. grandidentata* foliage. They rate the species used in their tests in the following order of decreasing preference: *P. grandidentata*, *P. tremuloides*, *Salix* spp., *Betula lutea* (= *alleghaniensis*), *B. papyrifera*, *P. balsamifera*, and *Alnus* spp.

Very little is known about the feeding habits of *anxius* adults, but they were occasionally observed feeding on *B. papyrifera* leaves by Barter (1957). Britton (1922) says bronze birch borer adults (those attacking birches) fly about and feed to some extent on the foliage of willow, poplar, and probably birch.

We have not tried feeding *horni* adults anything besides *P. tremuloides* leaves in the laboratory, and *horni* was found in the field on no plant other than *tremuloides*. Aspen leaves undoubtedly comprise the major portion of the adult *horni* diet, which is probably true for *g. liragus* also.

A. pensus, on the other hand, did not readily consume the foliage of aspens. Because they have been collected on the foliage of alders, but not on other plants, one would expect them to show some specificity for alder leaves. However, the only foliage which they seemed to eat readily in the laboratory was that of *Salix* spp. Very little testing with alder was possible, however, as the beetles were maintained in Ann Arbor, where alders are not readily available. Usually, *pensus* adults did not survive for more than a few days, no matter what kind of foliage they were provided. Adults of other species kept in the same controlled environment chambers survived exceptionally well (at 70 percent relative humidity; day temp 75°, night temp 60° F). The poor survival of *pensus* adults may have resulted because of a failure to provide the proper temperature and humidity for pupal development.

Dispersal

Nothing has been written about the dispersal capacities of *g. liragus* or *anxius*, and little is known about the dispersal of any *Agrilus*, including the ones that are naturalized pests in the United States. Heering (1956) has apparently made the only attempts at release and recapture studies with marked *Agrilus*. However, as only 200 *A. viridis* adults were released he was unable to recapture enought to give a reliable result.

Although *Agrilus* beetles may be capable of flying considerable distances, they probably do so only rarely. In rearing and maintaining these beetles in the laboratory we have seen nothing which would indicate the existence of any sort of antagonistic mechanism by which "flight exercise" acts as a releaser for feeding or reproductive activity as has been demonstrated for some aphids (Kennedy and Booth, 1963) and scolytid beetles (Graham, 1959, 1961). If they flew only far enough to encounter suitable hosts, they would usually be staying quite near the places where they emerged.

Host Selection

Following the period of reproductive maturation the adults are attracted to the hosts which have the particular attributes making them suitable for mating and oviposition. Many Agrilus and other Buprestidae seem to show a strong tendency to select hosts which are well exposed to sunlight. Consequently, those which live on trees are most active at forest edges or in park-like stands.

ANXIUS AND G. LIRAGUS. Generally, anxius females are said to oviposit on the sunny sides of trees and on those most exposed to sunlight. However, Barter (1957) found that the photopositive tendencies of anxius can be overridden, to some extent, by other stimuli, presumably olfactory ones. Barter says that when the shady sides of trees are wounded, females oviposit there rather than on the unshaded side. He concluded that the olfactory response is often stronger than the photopositive response.

Anderson (1944) came to similar conclusions. During the first season of his two-year study he found no deviation from the commonly accepted idea that trees exposed to full sunlight attract significantly greater numbers of anxius and g. liragus than shaded ones. Using a 30 second counting interval Anderson found an average of 2.6 beetles per unshaded tree, while only 1.8 were found on shaded trees. When the experiment was repeated the following year, however, he found that the count for unshaded trees did not differ significantly from that for shaded trees. During the first season, trees with the tops broken off by winter damage were abundant, but such damage did not occur during the second year. Anderson thinks that greater numbers of weakened hosts were available during the first season, allowing g. liragus to make a selection for those more exposed to sunlight. His conclusion is that the physiological condition of the host is more important than its degree of exposure to sunlight.

There may be sexual differences in the photopositive response, but little has been done so far to account for the possibility. Males and virgin females may be more photopositive than ovipositing females. Females ovipositing on fallen trees are apt to work along the sides of stems on days when males orient more towards the upper surface.

One is prone to confuse the effects of light and temperature. It seems quite likely that these beetles will appear to be more photopositive on relatively cool days (but still above 70° F) than on hot days. An observation made in 1964, during studies of anxius behavior, illustrates this point. In order to concentrate the beetles on bolts cut from freshly-felled birches, the tops and other unused parts of the birches were pulled well into the shade. This slash, nevertheless, attracted some of the beetles, and the bolts under observation, which were in full sunlight, attracted only moderate numbers of them. That day the temperature maximum was 85° F (U.S. Weather Bureau, 1964; Stambaugh, 15 July) and the sky was clear, so that temperatures may actually have been too high for the insects to remain for extended periods in the direct sunlight.

In another of Anderson's (1944) experiments, the attractiveness of 7 types of host material was evaluated by tallying the numbers of adult g. liragus on each aspen test tree during a 30 second counting interval. Observations were made between 10 AM and 3 PM on sunny days when the shade temperature was between 75° and 90° F. His results are presented in table 4, and it is quite evident that injured trees are more likely to be attacked than uninjured ones. Barter (1957) found this to be true for anxius also. From Anderson's data (table 4) one may also surmise that standing trees are more attractive to g. liragus than similarly treated trees which are felled. Both the topped trees and topped and girdled trees attracted significantly greater numbers of beetles than trees which were felled. Perhaps this occurred because the standing trees

Table 4. Attractiveness of various types of *Populus tremuloides* host material to *Agrilus granulatus liragus*.[a]

Condition of Host Trees	Average Number of Beetles per Tree per Observation[b,c]	Number of Observations
1. Vigorous	0	67
2. Suppressed	0	21
3. Girdled	0.1	54
4. Topped	1.9	54
5. Topped and girdled	2.8	27
6. Felled and lopped	1.0	27
7. Felled, not lopped	1.3	27

[a] Modified from Anderson (1944).

[b] The values are corrected so that each represents the number of beetles observed per 17 ft^2 of bark area, the average for all test trees.

[c] The only statistically significant differences are those between numbers not included within the span of a single vertical line.

were more fully exposed to sunlight than felled ones. In any case, these results could be misleading because standing trees rarely are as decisively injured by natural factors as are trees which are artificially topped or topped and girdled. The only natural injury which is really comparable occurs when trees are blown over. Less decisive natural injuries occur to standing trees when the tops are broken by winter ice damage or when the tops of already decrepit trees break where the wood exposed by repeated insect attack and disease becomes dry and brittle. Aspens are frequently victims of this type of injury, since the wood of these species is not particularly tough, and because they are often severely attacked by wood borers like *Saperda calcarata* and fungal parasites like *Hypoxylon pruinatum* for a period of years before they finally succumb.

One might also conclude from the data of table 4 that both suppressed and vigorous trees are unattractive to g. *liragus*. In testing this more thoroughly, Anderson used an extended observation period of 14 days, to detect occasional beetles that might be attracted to the trees. This was facilitated by placing sheets of fly paper on the trunks of 10 paired aspens, each pair composed of a vigorous and a suppressed tree. During the 14 day observation period 18 beetles were caught by the fly paper on suppressed trees, but none were caught on vigorous trees. It is apparent that g. *liragus* is able to detect trees which are in poor condition, whether or not they have been wounded. The stimulus is undoubtedly olfactory, and is presumed to arise from the decomposition of substances in the bark or phloem. The attractiveness of the host may, in turn, depend upon the rate of decomposition, which is no doubt enhanced by injury.

HORNI. Theoretically, the kind of host selection exhibited by *anxius* and *g. liragus* should allow adult feeding to be separated from the activities involved in host selection. If this is true, then there might not be any highly developed specificity shown by feeding adults. In the late 1800's, buprestid collectors clearly recognized that the identity of an *Agrilus* larval host was not necessarily indicated by the kind of foliage the adults are taken on. Perhaps this point is over-emphasized, because the adults of some kinds of species, like *horni*, may show more specificity in feeding, because feeding may be involved in the host selection process. *Agrilus horni* does not fly directly to the stems of aspen suckers, but instead lands on the foliage. The adults of this species usually feed before moving onto the stem where mating and oviposition occur. Whether or not they always feed before crawling from the foliage to the stem is not known. Nord et al. (1965) found that after caged *horni females* oviposit they move up to the foliage of suckers, resting and feeding for about 10 minutes before decending to lay another egg. Under natural conditions the females may usually ascend the stem following oviposition and fly to another sucker before feeding.

A. horni can maneuver with agility in flight, and can hover before landing. Their flight behavior indicates that they probably recognize aspen foliage before landing on it. If so, olfaction is clearly part of the recognition process. If the odors which direct them to the host do not, at least in part, emanate from the foliage, one would expect them to land frequently on the foliage of plants other than *Populus* spp. This was observed only once, when a male which had just mated flew from *P. tremuloides* sucker to a fern next to it, staying briefly before he flew back to the same aspen sucker and began feeding.

To go no farther than suggesting that *horni* recognizes its host by some characteristics of the foliage would be forming a hypothesis of very little value. Obviously, other factors must strongly influence the host selection of these beetles, as they do not live on just any species of *Populus*, or just any *P. tremuloides* sucker.

Previous Studies. Fowler (1963) studied the relationship of height, age, and stand density of aspen suckers to infestation by *horni*. He counted the number of infested and uninfested suckers on systematically located millacre quadrats. A graph of Fowler's data (fig. 20) appears to indicate that the unit-area density of *horni*-infested suckers is rather directly related to the unit-area density of all suckers.[1] However, it is not necessarily true that unit-area densities *per se* of the aspen suckers were the important variables affecting the infestation levels throughout Fowler's study area. It seems likely that some of the lower stand density values can be attributed to parts of it where the initial establishment of suckers was poor because of severe competition with other plants which dominated. Besides patches of sweet fern (*Myrica asplenifolia* [=*Comptonia peregrina*]), leather leaf (*Chamaedaphne calycultata*), and blueberry (*Vaccinium* spp.), there were young red pines (*Pinus resinosa*) scattered about. Quadrats with high sucker counts, on the other hand, may simply have occurred in places where some of the suckers were not shaded by other plants. In fact, high-count quadrats probably fell where suckers were clumped (fig. 21), and sucker clumps probably had originated in spots that were left denuded after the 1957 fire. Fowler (1963) notes that when infested suckers were associated with clumps, they were usually at the outer edges of them. A majority of the infested suckers in this may have occurred at the outer edges of clumps. Therefore, the contagion evident in the distribution of infested suckers may have resulted from strong contagion in the distribution of suckers suitable for oviposition.

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[1] A much more detailed analysis of the data is presented by Carlson (1968).

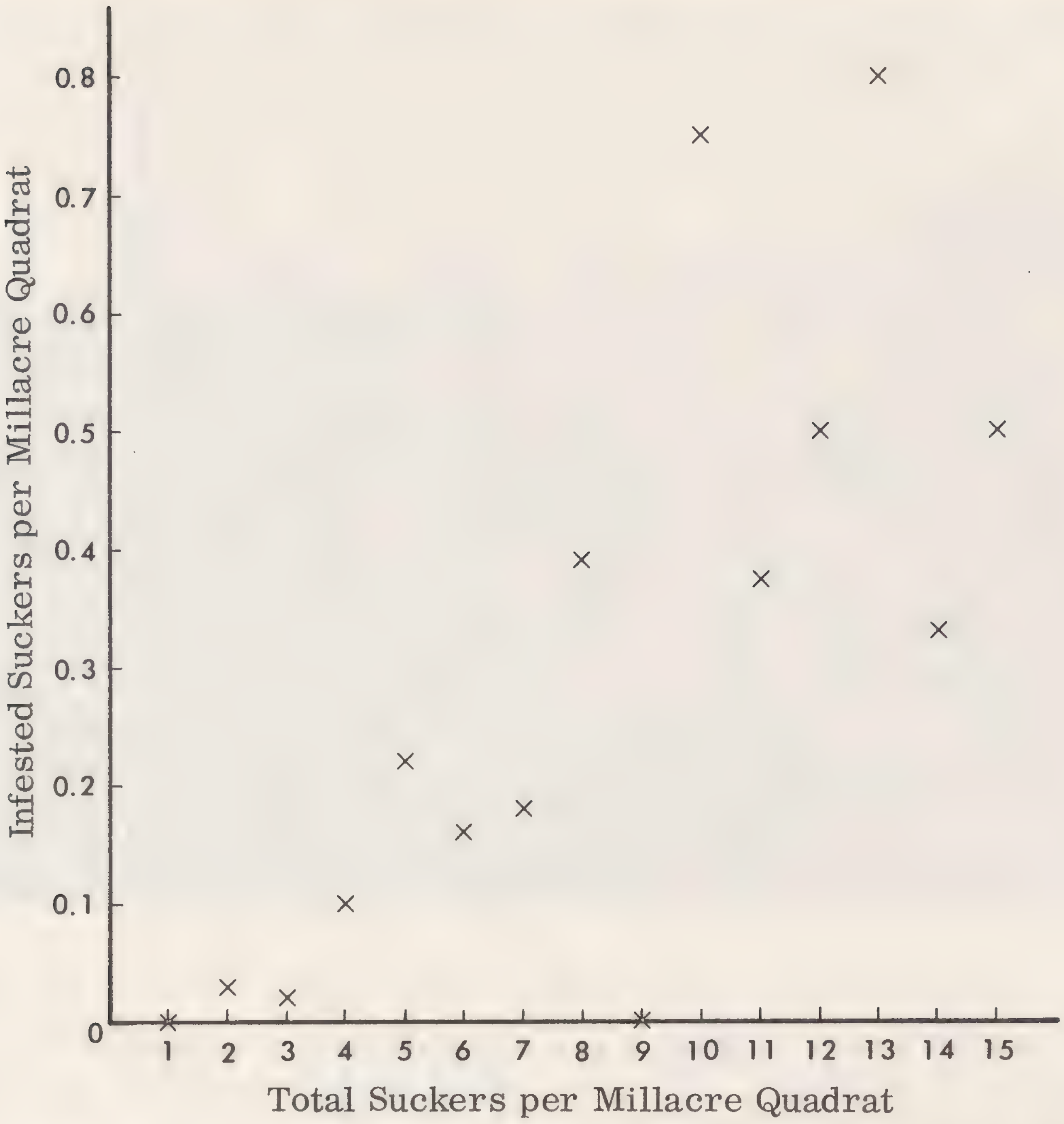

Fig. 20. Unit area density of horni-infested Populus tremuloides suckers as a function of stand density of all tremuloides suckers in the area sampled by Fowler (1963).

New Studies

Methods. The possibility that some contagion in egg distribution could occur independently of the distribution of suitable hosts has not been overlooked. In the spring of 1964 an area with an evenaged stand of aspen suckers was selected for studying this problem. It is an area near Beechwood, Michigan, where furrowing for the planting of pines had caused prolific root suckering by scattered, mature Populus tremuloides, some of which were still standing, while others had been pushed over (fig. 22).

Because the problem involved determining the spatial distribution of infested or egg-bearing suckers in relation to each other, there was little need for using standard sampling methods for estimating density (i. e. stems/unit area). Instead, it was decided that the problem could be best approached by using distance measurements as indicators of spatial relationships. The two variables measured were: (1) the distance from predetermined sampling points to the nearest infested or egg-bearing sucker (DNS) and (2) distance between each infested or egg-bearing sucker and the nearest neighboring infested or egg-bearing one (DNN). Sampling points were located systematically. Five plot centers were established, four at the corners of a 400 foot square and one in its center and also approximately centered within the study area.

Around each of the plot centers, 8 sampling points were established on a circle with a 50 foot radius. Sampling point number 1 was always located due north of the plot center, and the others were located at subsequent azimuthal intervals of 45 degrees. Sample distances were measured with a 100 foot tape.

Fig. 21. A spot in the study area of Nord (1962) and Fowler (1963), showing the clumped distribution of Populus tremuloides suckers and abundance of competing vegetation (from Nord, 1962). The aspen suckers occurred under similar conditions throughout much of the area.

Fig. 22. Agrilus horni study area near Beechwood, Michigan. The stand of Populus tremuloides suckers, which is relatively uniform in distribution, developed following furrowing for the planting of pines. Equipment used in the furrowing operation pushed over many of the mature aspens.

The Wilcoxon matched-pairs signed-ranks test (Siegel, 1956) was used for analyzing the data. Discussion of the results is deferred until later, where the results of a number of analyses are discussed together.

While evenaged sucker stands are best for studying the distribution of eggs by females, independent of sucker distribution, they are not well suited to studying the sucker size selection of horni females. For this, unevenaged areas are more appropriate. Unevenaged sucker areas occur in the ecotones between aspen forests and open fields or in park-like stands where clones or multiclone groups are apt to stand isolated, annually producing some suckers at their edges. Such areas are also of particular interest because they harbor more perpetual infestations than do evenaged stands. Devising sampling techniques for unevenaged areas was problematical, however. The most perplexing difficulty is that in these areas the zone in which the horni infestation occurs represents a rather small proportion of the ecotone area. Hence, it is difficult, if not impossible, to devise a random sampling scheme that is efficient. Even a systematic approach is difficult to contrive because the habitat of interest is usually distributed in a rather irregular manner. Therefore, the usual kinds of systematic procedures are not applicable.

The compromise devised cannot be considered ideally objective, but that does not seem to greatly impair its value. The sampling was carried out by proceeding along the edges of the clumps or closed stands of larger aspens and selecting the first 6 ft sucker encountered as a plot center. In turn, the 7 ft, 5 ft, 4 ft, 3 ft, 2 ft, and 1 ft suckers nearest the 6 ft one were selected[1].

The distance between the 6 ft sucker and each of the others (D_6) was measured. Before the suckers were chopped free at their roots and examined for eggs, the distance to the nearest neighboring sucker in the same height category (DNN) was measured and recorded. Only the first set of suckers selected was examined for horni eggs. Besides tallying the numbers of eggs and noting their positions, we also recorded the basal diameters of the suckers (DAB).

Successive plots were always separated by at least 3 times the maximum D_6. Six foot suckers were chosen for the sampling centers because they were near the upper size limit for suckers which would bear horni eggs. Consequently, choosing a 6 ft sucker would insure that sampling would include areas where suckers above the upper size limit occurred, while still keeping it within areas that were likely to be horni habitat.

This sampling method was employed in one area near Kenton, Michigan and in another near Phelps, Wisconsin. Analyses of the data chiefly involved the use of chi-square comparisons and graphic procedures. Expected values (E_x) for the chi-square analyses were derived from expectancy factors (E_f), which are weighting factors based upon D_6 and DNN (collectively, D values) measurements. The basis for the computation of expected values is the assumption that the abundance of suckers in a particular size class is inversely related to the area of a circle which has a radius equal to the average D value for the class. Hence, density is proportional to $1/D^2$. In deriving the E_f values it was anticipated that DNN measurements should account for any clumping tendency among suckers of the same age. On the other hand, the D_6 measurements should account for any stratification that existed, such as gradients in the positions of suckers relative to those of other sizes. E_f values are computed simply by dividing the $1/D^2$ value for each size class by the total for all

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[1] Each height class had a ±0.5 ft interval.

classes (giving each E_f relativity to all others). The expected numbers of egg-bearing suckers are derived by multiplying the total observed number of egg-bearing suckers by each E_f value.

One set of chi-square comparisons was made for height classes, and in another set the numbers of egg-bearing suckers were apportioned into DAB classes (table 6). Diameter class (DAB) values for the latter comparisons were computed from regressions of DAB over sucker height by substituting the values for the height class limits into the equation and solving for DAB.

To compare height and DAB as indicators of the suitability of suckers for *horni* oviposition, ratios of observed to expected values are used. This required the computation of additional expected values for a set of DAB classes with uniform limits. It was necessary to derive expected values for these uniform DAB classes indirectly, because there was no direct (significant) statistical relationship between DAB and D values.

In order that all ratios of observed to expected values have positive signs, it is necessary to adjust all expected values (E_x) upward so that none is exceeded by the observed (O_x) value for the same class. What was done, in effect, was to multiply all E_x values by the greatest O_x/E_x ratio occurring among all sucker classes (yielding $E_{x\alpha}$). The subsequently derived $O_x/E_{x\alpha}$ ratios can be used for making between-area data comparisons as well as for the height-DAB comparison mentioned above. Factors with similar uses are derived by dividing the total number of eggs (S) occurring on the suckers of each size class by the corresponding $E_{x\alpha}$ values.

Discussion. There were no significant differences between DNS (distance to nearest sucker) and DNN (distance to nearest neighbor) measurements for either the infested or the egg-bearing suckers at the Beechwood, Michigan evenaged sucker stand. Therefore, there is no marked tendency toward contagion in the distribution of either infested or egg-bearing suckers. Two obvious explanations are possible. (1) *A. horni* females may make a post-oviposition flight, before they re-alight and lay another egg. This sort of behavior should lead to a rather random distribution of eggs. (2) On the other hand, suckers which were suitable for oviposition and subsequent infestation may have been rather randomly distributed throughout the area.

The latter explanation seems to be the most logical. The few direct field observations made on *horni* females would indicate that they really do not fly very far before landing on another sucker. Nor is there any indication that a post-ovipoisition flight is an unvarying occurrence in a fixed behaviorial pattern. Nord et al. (1965) found that after ovipositing, caged *horni* females immediately crawled up the sucker stem and out onto a leaf. After spending about 10 minutes feeding and "resting," they might descend to lay another egg, and so on.

Under natural conditions *horni* females may usually fly to another sucker after each egg is laid. It may be uncommon for them to feed on a sucker just after ovipositing on it, particularly if feeding is an integral part of the host selection process. In the Beechwood area only a few suckers were found with two *horni* eggs, and only one had three. When more than one egg had been placed on a given sucker, there was usually no way of knowing from their appearance if they had been deposited at about the same time or at different times. Unlike the Beechwood area, the egg-bearing suckers in the Phelps and Kenton areas usually had more than one egg (average 2.5) and one had a surprising total of 15 (table 5). When the difference between the latter areas and the Beechwood area are considered, it is only reasonable to conclude that the oc-

Table 5. The occurrence of Agrilus horni eggs in the Kenton and Phelps areas on Populus tremuloides root suckers in height classes of 1 to 7 ft.

Sucker Height Class (feet)	Suckers Sampled	Suckers bearing no eggs	Suckers Bearing Eggs								Number of Eggs	
			Categorized by Number of Eggs per Sucker							Total	Total	Average per Egg-Bearing Sucker
			1	2	3	4	5	9	15			
1	30	29	1							1	1	1.0
2	30	23	3	3	1					7	12	1.7
3	30	21	3	1		3		1	1	9	41	4.5
4	30	16	6	4	2		2			14	30	2.1
5	30	20	3	3	3			1		10	28	2.7
6	30	22	5		3					8	14	1.7
7	30	26	2	1		1				4	8	2.0
All	210	157	23	12	9	4	2	2	1	53	133	2.5

currence of more than one egg on a single sucker is usually not an indication that they were laid in sequence by the same female. Instead, what seems to be indicated is that some suckers were far more suitable for horni oviposition than others, even of the same size. Moreover, in the Phelps and Kenton areas the horni habitat was restricted to a very narrow zone, and movement along it probably resulted in these beetles contacting suckers in particular locations more frequently than others. The most reasonable conclusion seems to be that when suckers in these particular locations were otherwise favorable for oviposition there were a number of eggs laid on them.

Sucker size should be an important factor affecting the distribution of eggs by horni females and/or the survival of the larvae. In both height and DAB chi-square comparisons the difference between the observed and expected distribution of eggs is highly significant (table 6). The relationship of egg occurrence to DAB is more sensitive than that with sucker height (figs. 23-26).

The Kenton trend line of $O_x/E_{x\alpha}$ over DAB (fig. 24) shows a double peak, but the second peak is reduced in the graph of $S/E_{x\alpha}$ over DAB (fig. 26). This suggests that in the Phelps area the suckers most likely to elicit horni oviposition had somewhat larger diameters than those in the Kenton area. This appears to be true despite the fact that the abundance of small suckers relative to those of larger sizes was greater in the Phelps area. Examination of the data on egg placement for the two areas yields the most likely reason for this difference. In the Phelps area more eggs were located in association with moss than on other kinds of deposition sites. Most of those Phelps area eggs deposited in association with moss occurred on the 0.6 and 0.7 inch suckers (all but 2 out of 21), and these two DAB classes were the source of the greatest difference between the areas. Therefore, it seems very likely that the occurrence of mosses on these suckers in the Phelps area is responsible for the positive skewing of the trend lines (figs. 24, 26) as compared to the more negatively skewed ones for the Kenton area.

Inasmuch as factors independent of sucker size, such as the occurrence of mosses, affect horni oviposition, even two areas with nearly identical arrays of sucker sizes will not necessarily have similar frequency distributions for those bearing eggs. In general, however, the data do strongly indicate this much: suckers between 0.3 and 0.9 inches DAB are most likely to elicit oviposition.

Table 6. Chi-square comparison of observed and expected size-class frequency distributions of Populus tremuloides suckers bearing Agrilus horni eggs in the Kenton and Phelps areas.

Area	Height Class (feet)	Egg-Bearing Suckers Observed (O_x)	Egg-Bearing Suckers Expected $(E_f\ X\ \Sigma O_x)$	χ^2	DAB Class (inches)	Egg-Bearing Suckers Observed (O_x)	Egg-Bearing Suckers Expected $(E_f\ X\ \Sigma O_x)$	χ^2
Kenton	1	1	8.13	6.25	< 0.211	2	8.13	4.62
	2	4	6.83	1.17	0.222 - 0.358	3	6.83	2.15
	3	5	5.16	0.00	0.359 - 0.505	10	5.16	4.54
	4	9	3.57	8.26	0.506 - 0.652	5	3.57	0.57
	5	4	2.26	1.34	0.653 - 0.808	6	2.26	6.19
	6	3	1.32	2.14	0.809 - 0.955	2	1.32	0.23
	7	2	0.73	2.21	> 0.955	0	0.73	0.73
Total		28	28.00	21.37**		28	28.00	19.03**
Phelps	1	0	11.50	11.50	< 0.179	0	11.50	11.50
	2	2	6.31	2.94	0.180 - 0.287	2	6.30	2.93
	3	3	3.59	0.10	0.288 - 0.395	3	3.59	0.10
	4	6	2.10	7.24	0.396 - 0.503	8	2.10	16.58
	5	7	1.26	26.15	0.504 - 0.611	4	1.26	2.40
	6	6	0.77	35.52	0.612 - 0.719	4	0.77	13.55
	7	2	0.47	4.98	> 0.719	3	0.47	13.62
Total		26	26.00	88.43**		24[†]	24.00	60.68**

[†] Total differs from that for height comparison because two DAB values are missing.

** Statistically significant at the 0.01 probability level.

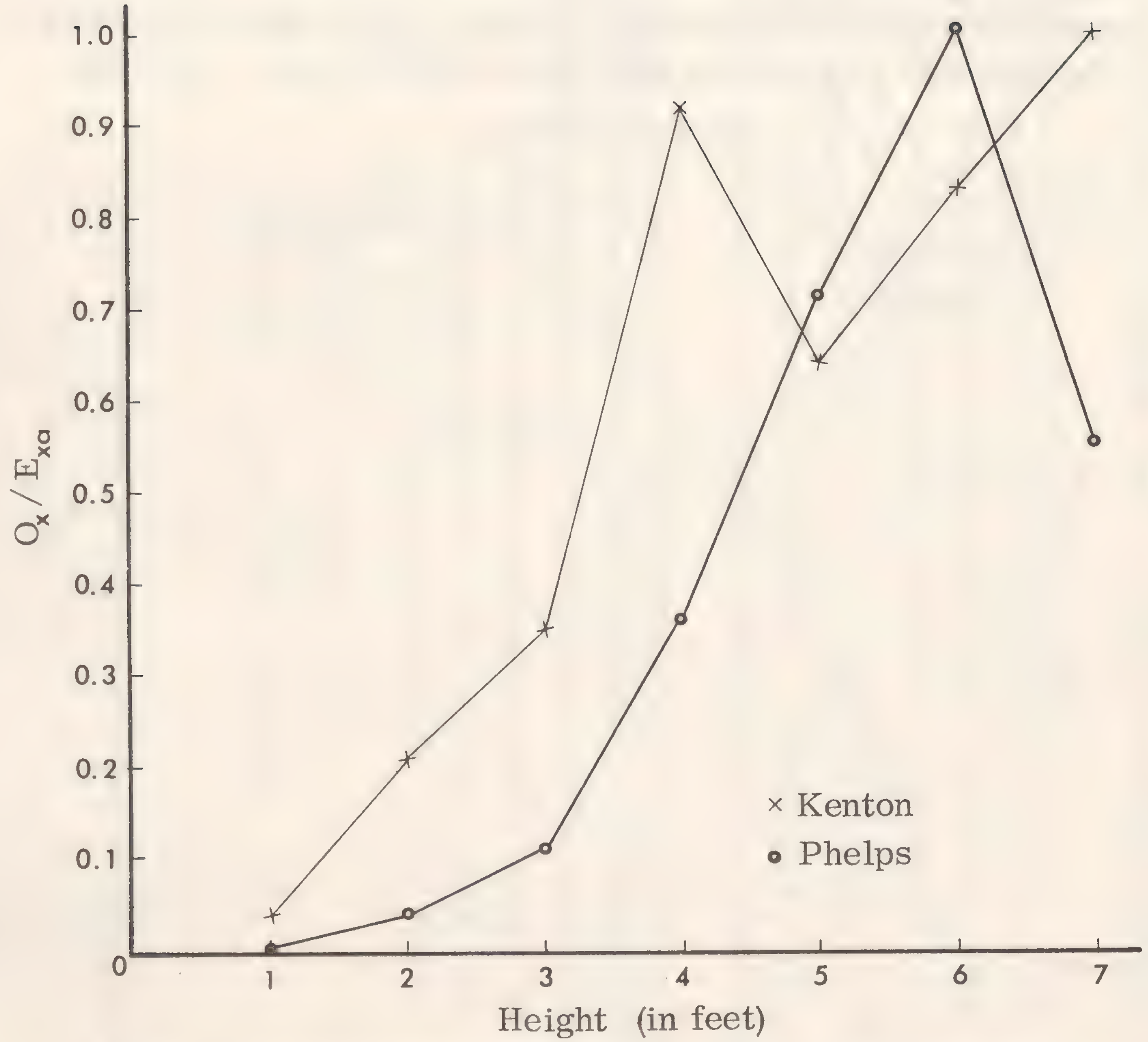

Fig. 23. Distribution of Agrilus horni eggs: ratio of the observed (O_x) and adjusted expected numbers (E_{xa}) of Egg-bearing suckers for each sucker height category plotted as a function of sucker height.

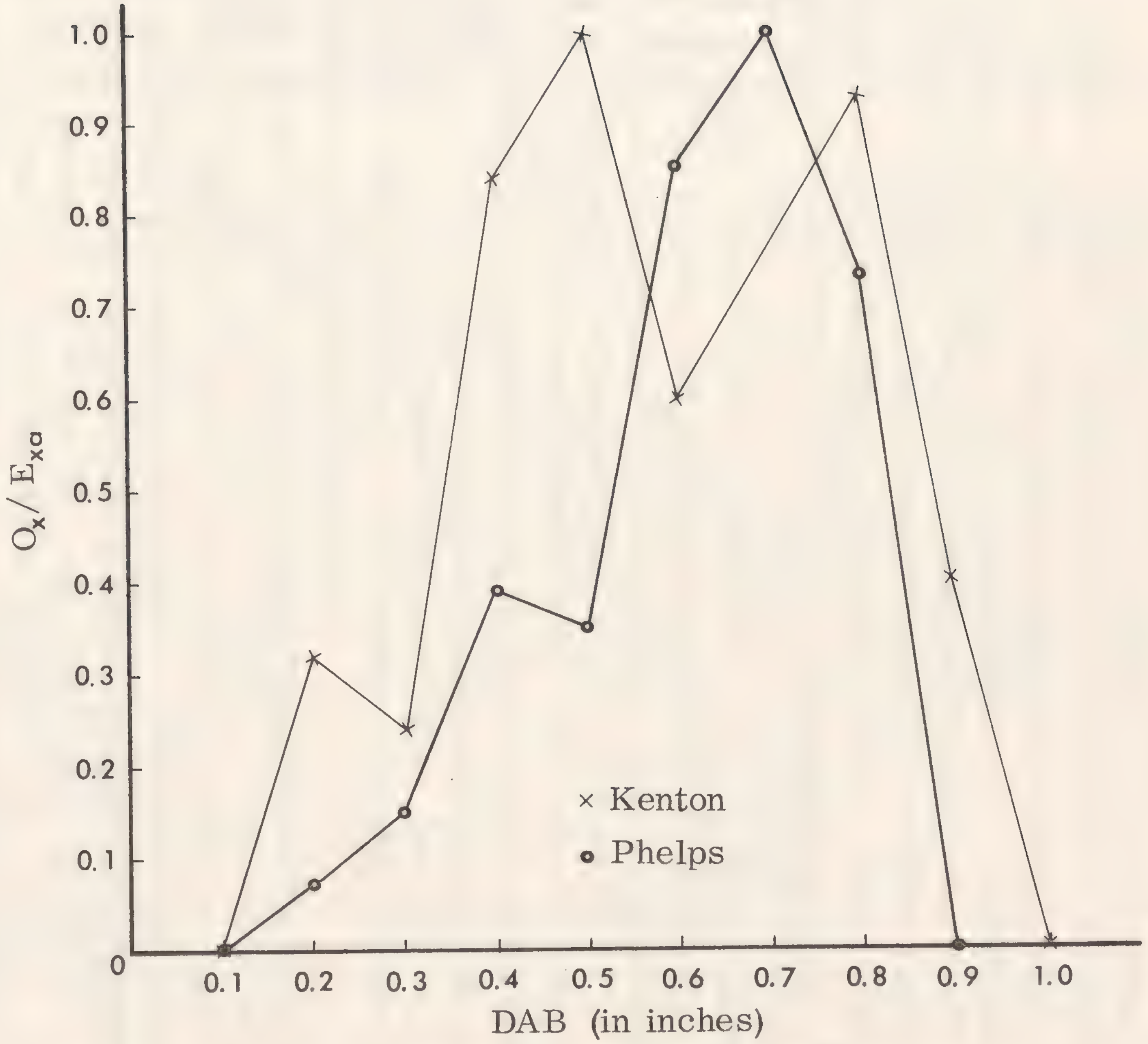

Fig. 24. Distribution of Agrilus horni eggs: ratio of the observed (O_x) and adjusted expected numbers (E_{xa}) of egg-bearing suckers for each sucker DAB (diameter at base) category plotted as a function of sucker DAB.

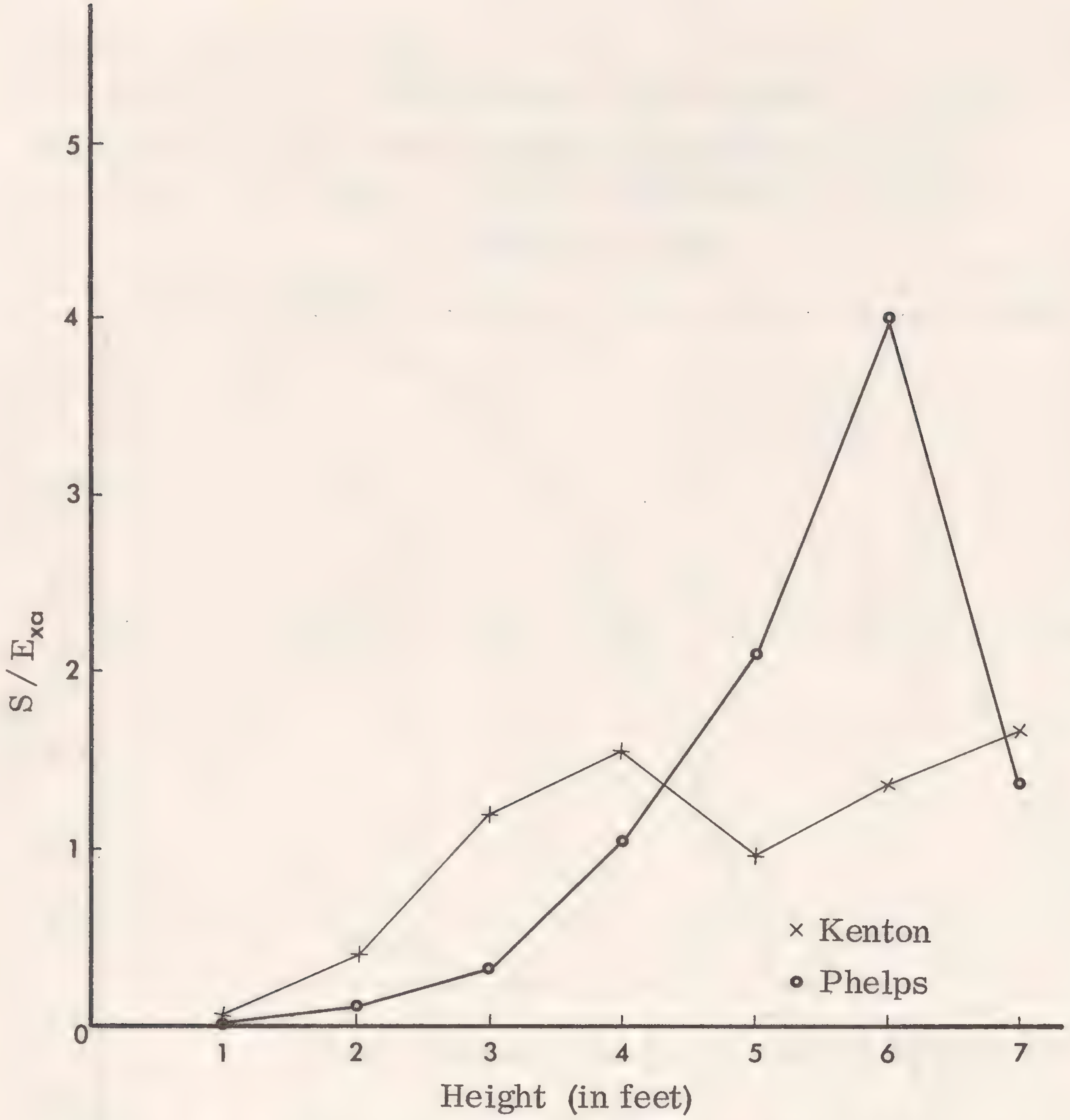

Fig. 25. Total *Agrilus horni* eggs (S) found on egg-bearing suckers of each height category, divided by the adjusted expected numbers ($E_{x\alpha}$) of egg-bearing suckers per category and plotted as a function of sucker height.

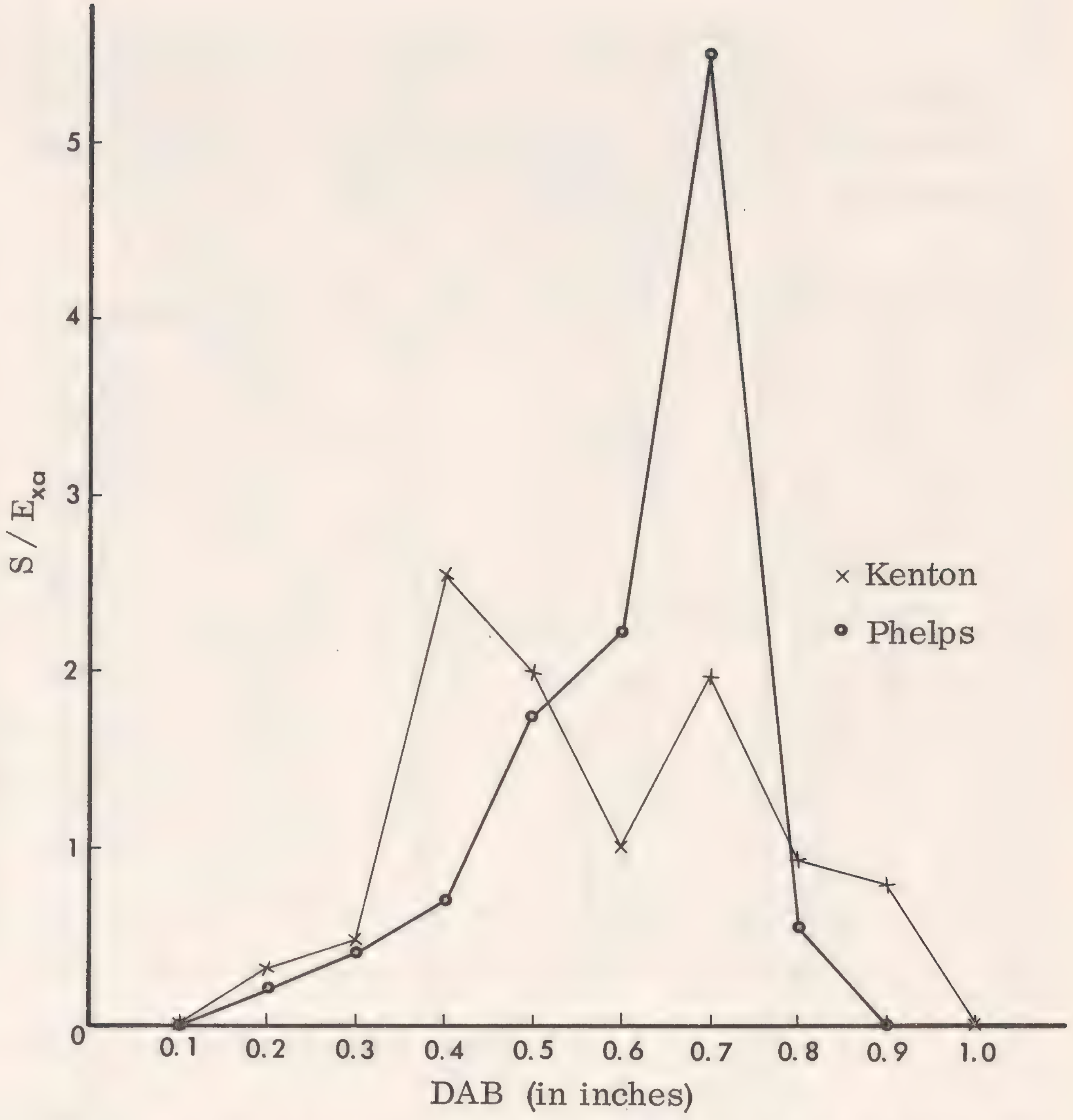

Fig. 26. Total *Agrilus horni* eggs (S) found on egg-bearing suckers of each DAB (diameter at base) category, divided by the adjusted expected number ($E_{x\alpha}$) of egg-bearing suckers per category and plotted as a function of sucker DAB.

Without data on the DAB frequency distribution of a stand to compare with that of its egg-bearing suckers, one probably would not come to the same conclusion. In other words, the information obtainable by sampling at random in respect to sucker size and tallying only data pertinent to egg-bearing suckers would be quite different from that presented above. Hypothetical numbers of egg bearing suckers for Phelps and Kenton are plotted in figure 27a, and represent what might have been expected from a random sample of 1000 suckers in each area, as calculated by Carlson (1968). Figure 27b shows that 2/3 of the egg-bearing suckers in the Phelps area would probably have been below 0.4 inches DAB, while a like proportion for the Kenton area should have been below 0.5 inches. Figure 27a agrees with *a priori* expectation for a random sample in that the curves are negatively skewed and have less pronounced maxima than those in figure 25. The negative skewedness of the former is due to the preponderance of suckers of smaller sizes (the "j" age-frequency distribution). A possible explantion for the disparity between the two curves is that *horni* tends to oviposit on suckers that may be somewhat above optimum size for survival of larvae as a natural compensation for the preponderance of suckers which possibly are below optimum size. A study of the relationship between sucker DAB, root size, and survival of *horni* larvae would, of course, be necessary for proving this hypothesis.

The mechanism which restricts *horni* egg placement to suckers within moderately narrow diameter limits is unknown, but it may be proprioceptive. Proprioceptors that could operate in measuring suckers could be located in the legs, antennae, or even the ovipositor. There are no obvious morphological features differing from those of either *anxius* or *g. liragus* that could be singled out as possible sites for the supposed proprioceptors. However, *horni* varies much less in size than either *anxius* or *g. liragus*, and the genetic basis for this lower variability may not be unrelated to *horni* host selection behavior.

In reference to *horni*, Graham et al. (1963) say that "the root-girdling *Agrilus* deposits its eggs on the bark either near the ground or sometimes a foot higher." Three inches above ground line is the maximum height at which we have found *horni* eggs under natural conditions. In fact, we found 150 eggs below the 1 inch level, while encountering only 34 above it, a highly significant statistical difference from the expected (table 7). All but 2 of the latter (table 8) were below the 2 inch level. Therefore, Graham et al. (1963) were probably mistaken in identifying anything at the 1 foot level as *horni* eggs.

The *horni* eggs were commonly deposited on rough bark (lenticels, cracks, flakes, etc.) against adventitious buds, against or beneath the leaves and stems of mosses which sometimes grow on the bases of the suckers (table 8). Oc-

Table 7. Chi-square comparison of the number of *Agrilus horni* eggs above and below the 1 inch level on the bases of *Populus tremuloides* root suckers.

Height above Ground (inches)	Number of Eggs		
	Observed	Expected	χ^2
0-1.0	150	92	36.56
1.1-3.0	34	92	36.56
Total	184	184	73.22**

**Statistically significant at the 0.01 probability level.

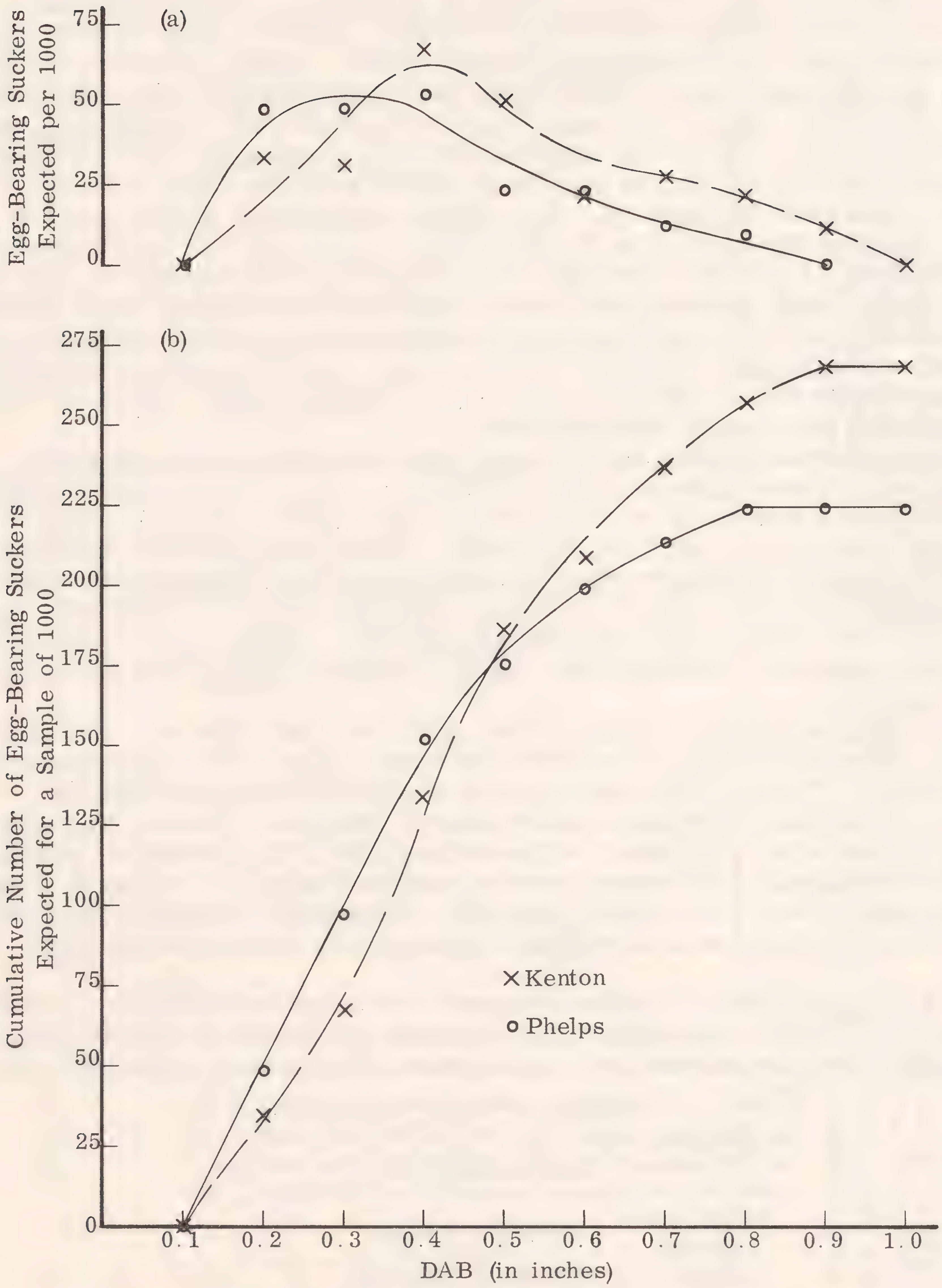

Fig. 27. Hypothetical distributions for Agrilus horni eggs: the number of egg-bearing suckers (a) and cumulative number (b) expected for random samples of 1000 Populus tremuloides suckers for areas near Kenton, Michigan (dashed line) and Phelps, Wisconsin (solid line).

Table 8. Position and situation of Agrilus horni eggs on Populus tremuloides: pool of data for 1964 (Beechwood area) and 1965 (Kenton and Phelps areas).

Height Above Ground (inches)	Eggs Situated on or Against:				Total
	Smooth Bark	Rough Bark (flakes, etc.)	Buds	Moss	
0	18	27	13	16	74
0.1 - 1.0	6	43	16	11	76
1.1 - 2.0	1	19	11	1	32
2.1 - 3.0	0	0	2	0	2
Total	25	89	42	28	184

casionally, they were also found on smooth bark, but most of those eggs were located at ground line where they had probably been partially supported by organic debri of some sort. A chi-square comparison between the height distribution of eggs laid on smooth bark and that for all other eggs shows them to differ significantly (table 9). While the number of eggs laid on smooth bark above ground line is less than the expected value, the reverse is true for the number observed at ground line.

Table 9. Chi-square comparison of positions of Agrilus horni eggs on smooth bark with positions of other eggs (pooled data from Beechwood, Kenton, and Phelps areas).

Height Above Ground (inches)	Number of Eggs					χ^2
	Observed			Expected[†]		
	Smooth Bark	Other	Total	Smooth Bark	Other	
0	18	56	74	10.06	63.94	6.27
0.1 - 1.0	6	70	76	10.33	65.67	1.81
1.1 - 2.0	1	31	32	4.35	27.65	2.58
2.1 - 3.0	0	2	2	0.27	1.73	0.27
Total	25	159	184	25.01	158.99	10.93*

[†] Expected = (observed column total ÷ grand total) × row total.

*Statistically significant at the 0.05 probability level.

Mating Behavior

FUNCTIONAL MORPHOLOGY

Aedeagus. Before entering the discourse on the behavior of individuals during courtship and mating, it will be necessary to describe some anatomical structures important in mating. Basing the interpretation on Lindroth and Palmén (1956), the aedeagus (fig. 28) of buprestid males is composed of an eversible penis (pe), which is sheathed by the tegmen. The tegmen is composed of the paired parameres (pa) and an unpaired basal piece (bp). The junction between the basal piece and the parameres is not evident in Buprestidae. Hence, the term parameres will be used to denote the part of the tegmen which is divided, the part often called the lateral lobes in buprestid taxonomic discourse. The latter, and the associated designation of the penis as the medi-

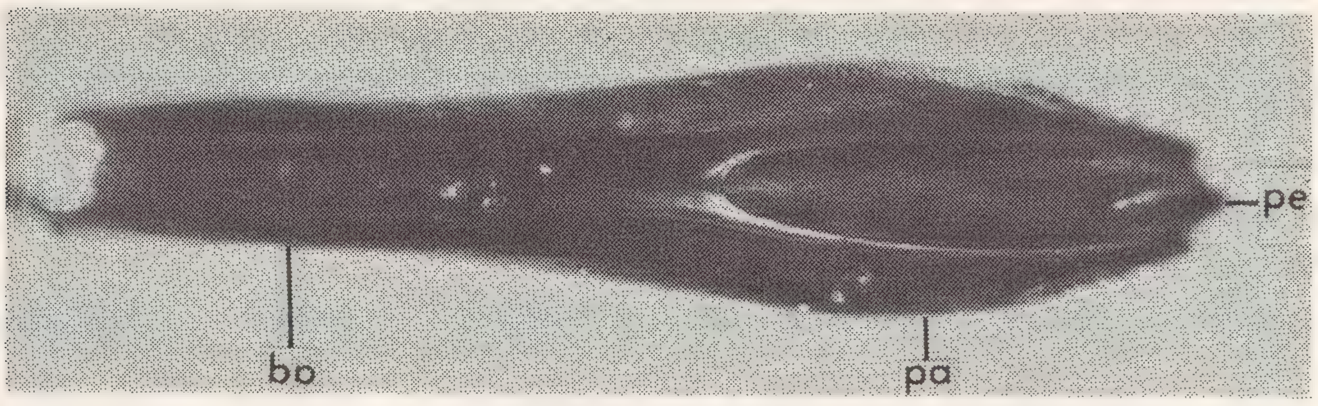

Fig. 28. Dorsal side of the aedeagus of *Agrilus granulatus liragus*; pe = penis, pa = parameres, and bp = basal piece.

an lobe, are not useful terms for functional descriptions.

On the ventral[1] side of the tegmen (figs. 5-8) of species in the *anxius* group, there is a trough or groove which extends from near its base to the tips of the parameres. It is very narrow at the base of the tegmen and gradually increases in breadth toward the apex, broadening most in *anxius*, but much less in *horni*. During coitus this groove receives the pygidial spine of the female, which serves to guide the aedeagus into position. The groove also appears to have functions connected with sexual recognition which are discussed later.

There is also a groove on the dorsal side of the aedeagus (fig. 28), although it is rather shallow in comparison to that on the ventral side. The penis is only slightly recessed below the dorsal surface of the parameres, which are rather flattened, and the groove extends basad of the parameres, sometimes nearly to the base of the tegmen.

Movements of the heavily sclerotized aedeagus appear to be controlled mostly by the large muscles that are directly attached to it. The ovipositors of buprestids, on the other hand, are not heavily sclerotized. As there are no muscles directly attached to them, they are principally hydrostatic organs.

Female Organs of Reproduction. The only interpretation of the morphology of a buprestid ovipositor known to us is that of Tanner (1927). Because the ovipositors of Buprestidae appear to differ from those of other Coleoptera, it seems best to employ his interpretation. After the homologies are worked out, it may be possible to use less burdensome terminology.

The ovipositor of species in the *Agrilus anxius* group (fig. 29) differs from the configuration shown by Tanner (1927) for *Chrysobothris debilis* Leconte in a single important way. The *C. debilis* ovipositor, which is similar to that of a *Buprestis* sp., has the bacula of the proctiger and coxite separated by the entire length of the valvifer baculum. Species in the *A. anxius* group have the bacula of the proctiger and coxite separated only by the thickness of the valvifer baculum. The valvifer baculum lies beside that of the coxite, and the two are nearly parallel, except at their bases, where the valvifer baculum intervenes between the bacula of the coxite and proctiger.

Figure 29 shows the *Agrilus anxius* ovipositor in its various attitudes. A comparison between fig. 29, c and d shows how the ovipositor can be likened to a tube within a mostly membraneous sac. The part of the ovipositor bearin the coxites will be referred to as the ovipositor tube. It appears that only this part of the ovipositor is actually extended from the abdominal cavity during oviposition.

During copulation the male aedeagus is inserted to the point where the tip

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[1] Ventral in the retracted position, as is traditional; not ventral *sensu* Lindroth and Palmén (1956).

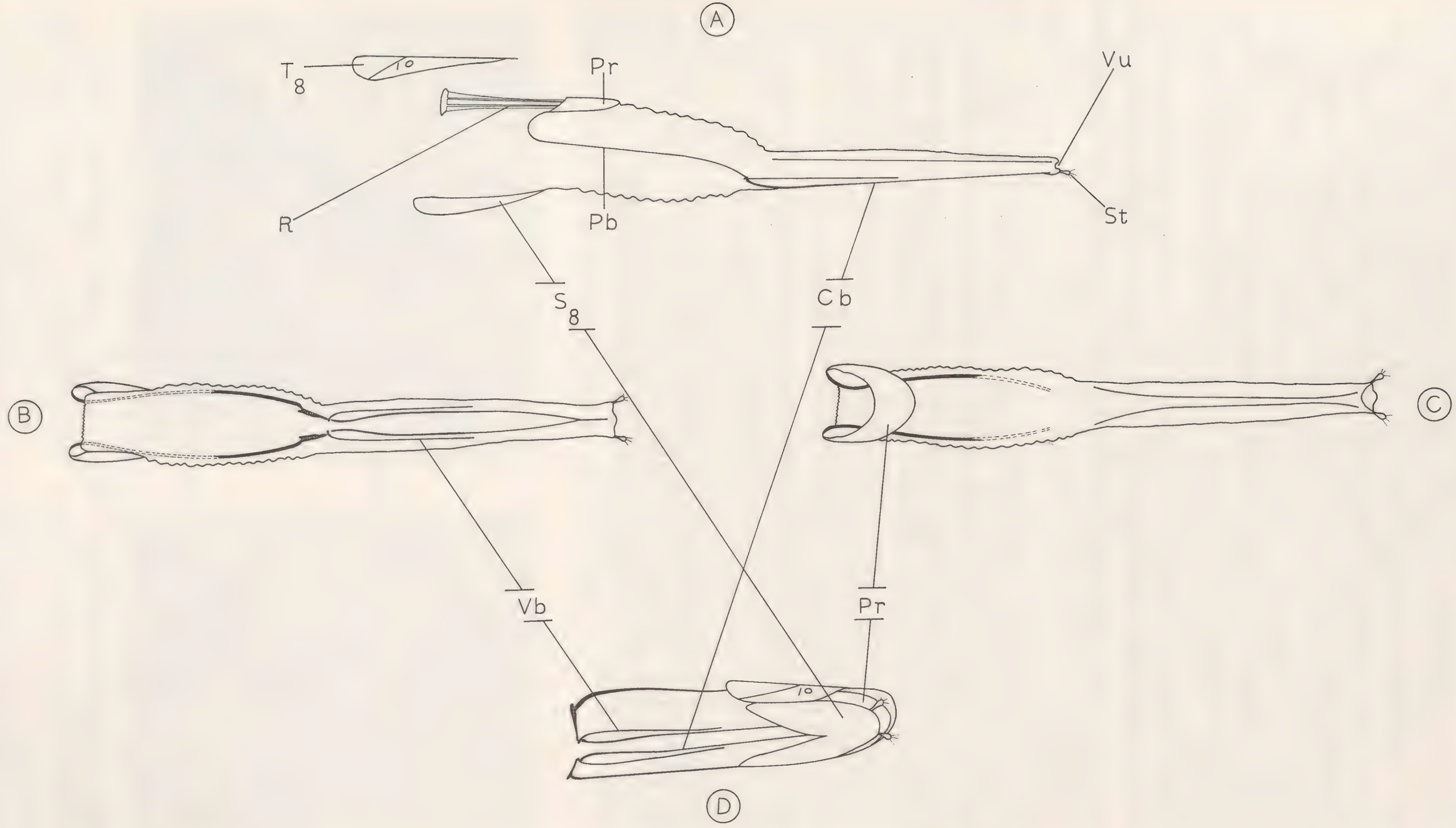

Fig. 29. Lateral (A), ventral (B), and dorsal (C) aspects of the ovipositor of *Agrilus anxius* in extended position (about X20). The degree of extension shown in A through C simplifies the illustrations, but ovipositing females do not appear to extend the ovipositor as completely. The view shown in D is ventro-lateral in retracted position. All views were drawn without the aid of a camera lucida. The symbols: T_8 = tergite 8, S_8 = sternite 8, R = rectum, Pr = proctiger, Vu = vulva, St = stylet, Pb = proctiger baculum, Vb = valvifer baculum, and Cb = coxite baculum.

of the female's pygidial spine rests in the basal end of the ventral groove on the tegmen. When the aedeagus is in this external position, its probable internal position in relation to the various bacula of the ovipositor tube is as shown in fig. 30. It is assumed that after this position is attained, the male everts the penis into the vagina (Va, fig. 31). The tip of the penis probably fits into the receptacle (Rp, fig. 31). The wall of the vagina has a complex, thickened structure which gives it great elasticity. It is therefore assumed that after the penis apex enters the receptacle, eversion of the penis continues until it is fully extended. It appears that the elasticity of the vagina may allow successful interbreeding between even the individuals at opposite size extremes in populations with extensive size variation.

After the penis is fully extended, the internal sac is evidently everted upward into the bursa copulatrix (Bc, fig. 31). The minute spinules surrounding the opening to the bursa apparently guide the sac into place. They probably also serve to hold the sac in place as insemination occurs.

BEHAVIOR OF MALES

Sexual Recognition. When a male (A)[1] mounts another individual (B), he almost immediately exserts his aedeagus, which at first projects backward, but then rotates downward and forward such that its apex contacts the tip of the abdomen of individual B. After the abdomen of B is contacted, the subse-

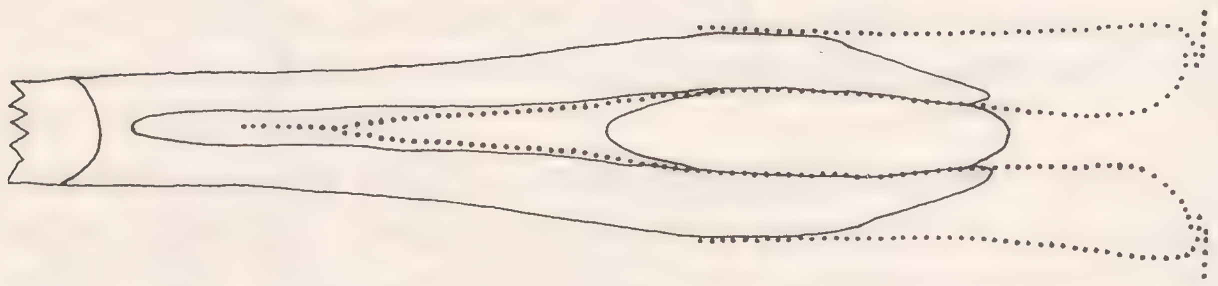

Fig. 30. Probable position of the dorsal side of the aedeagus (solid line) relative to the bacula of the ovipositor (dotted line) during copulation in *Agrilus granulatus liragus* (cf figs. 28 & 29).

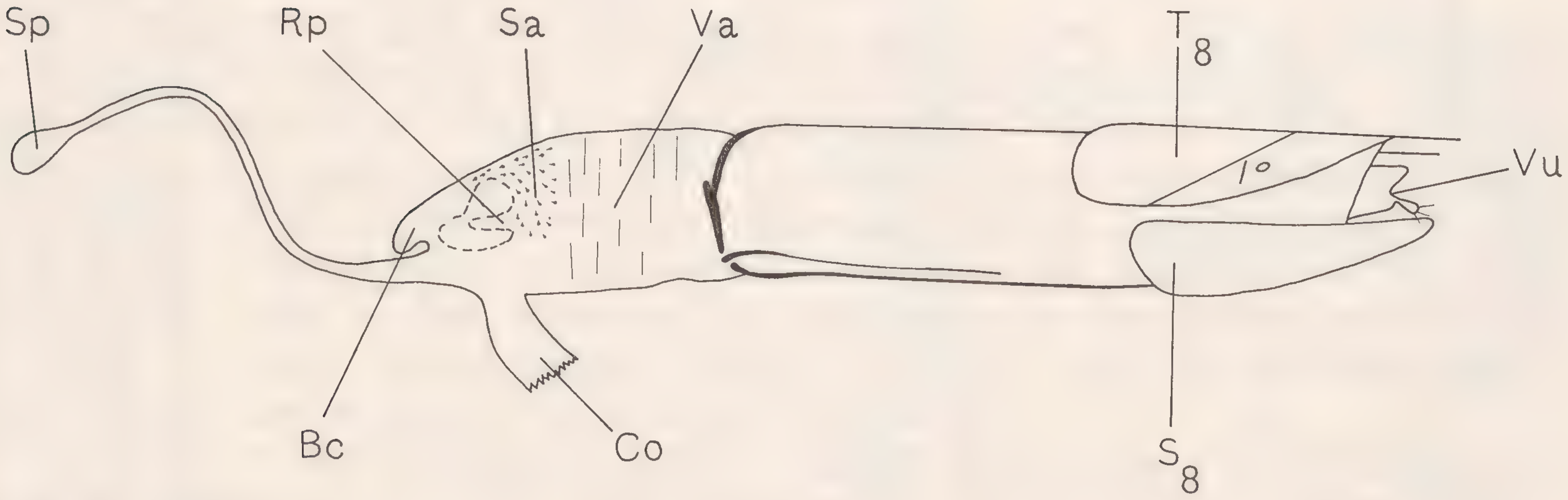

Fig. 31. Lateral view of the Agrilus anxius ♀ internal organs of reproduction (less ovaries) and ovipositor (retracted position); Sp = spermatheca, Rp = receptacle for penis apex, Bc = bursa copulatrix, Sa = spiculate area of vagina, Co = common oviduct, Va = vagina, T_8 = tergite 8, S_8 = sternite 8, and Vu = vulva. Drawn without the aid of a camera lucida.

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[1] Hereafter courting males are referred to as "A" and the individual being courted as "B."

quent behavior of the courting male (A) depends upon the position of the hind sternite of individual B. If the sternite is in lowered position, insertion and copulation ensue, provided B is a female. If B is a male, the tips of the aedeagi of both come into contact and male A dismounts quickly.

When the aedeagus dissected from a male was placed into the abdominal opening of virgin females, courting males responded to them just as they did to males, provided the aedeagus artificially implanted in the females had not moved to the side of the abdominal opening. Therefore, it appears that the responses of courting males are elicited by what they touch with the aedeagus. The observations were few, however, and only one observation was made on a male courting another whose aedeagus was removed. In this case insertion of the aedeagus occurred, and when the behavior of male A indicated that he was everting the internal sac, he was removed, whereupon the sac was revealed protruding from the tip of the penis.

When a courting male probes an individual not having the hind sternite in lowered position, the process of sexual recognition is somewhat more intricate. Before the behavior of courting males in this situation can be described, some sexually dimorphic structures of the last abdominal segment must be discussed. The role played by the female pygidial spine during insertion of the aedeagus has already been partially considered. Were this the only function of the spine, it would be difficult to explain its presence in males. Moreover, male pygidial spines are often somewhat longer (relative to body length) than those of females. The significance of this dimorphism seems to relate to the function of other sexually dimorphic structures of the hind segment. In both sexes the marginal sclerite of this segment is smooth and flattened, and a groove separates it from the sternite. The apex of the hind marginal sclerite of females is angled slightly upward, or beveled, with respect to the sternite (fig. 32). In males, however, its apex lies in almost the same structural plane to which the sternite conforms (fig. 33). The groove between the marginal sclerite and the apical part of the hind sternite seems to be somewhat larger in females than males, but this appears to be partly due to the differences in the angulation of the marginal sclerite.

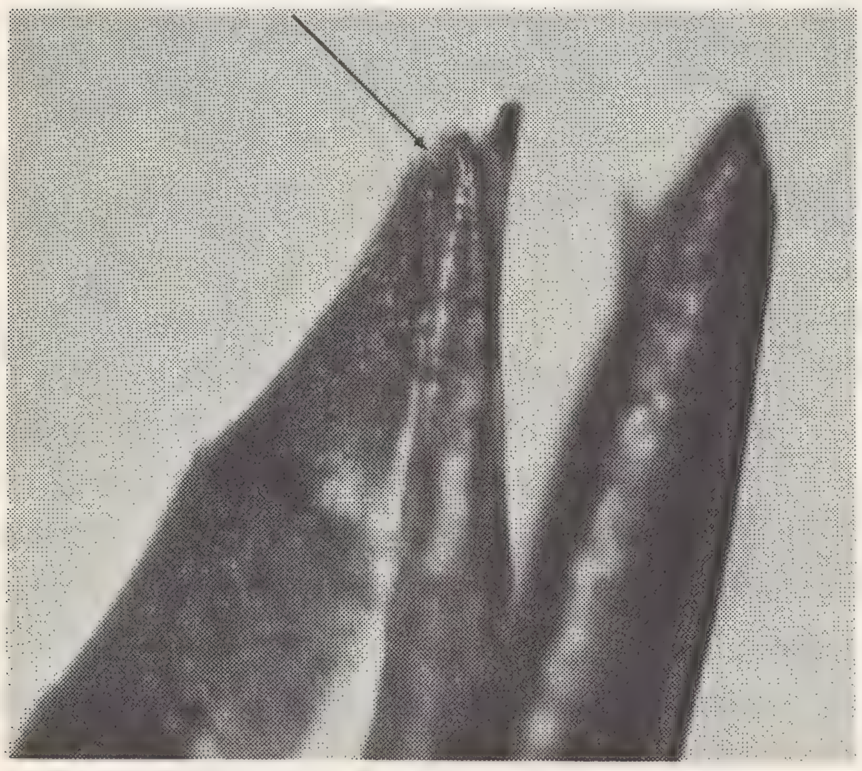

Fig. 32. Abdominal apex of Agrilus granulatus liragus ♀; arrow points to the groove between the marginal sclerite and sternite of the last segment.

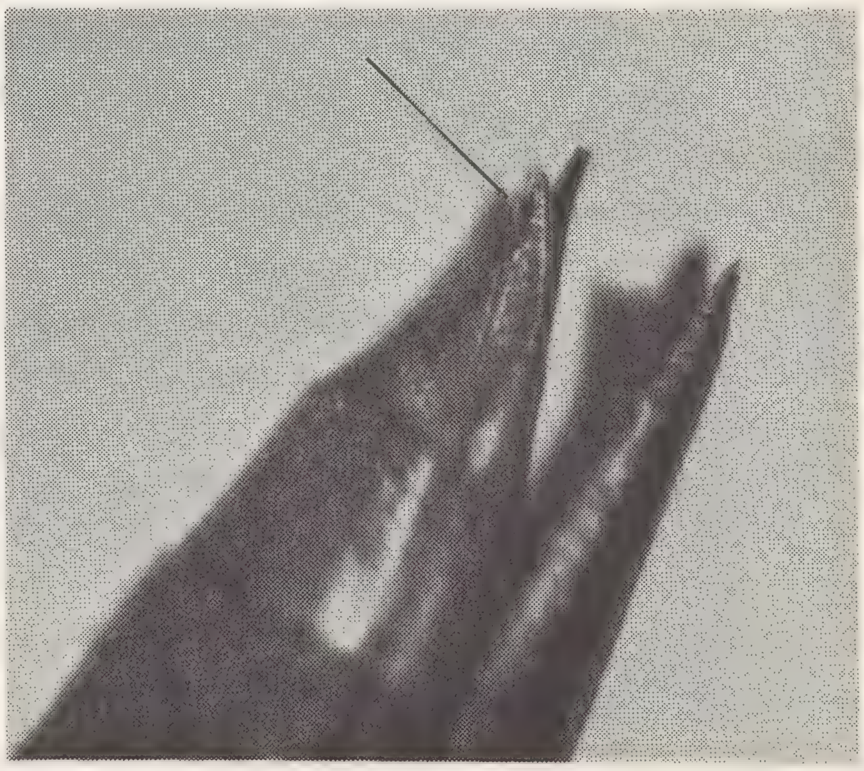

Fig. 33. Abdominal apex of Agrilus granulatus liragus ♂; arrow points to the groove between the marginal sclerite and sternite of the last segment.

Let us return to the situation in which a male probes an individual whose hind sternite is in the closed position. The tip of the aedeagus of A first touches the marginal sclerite of B at or near the point where it closes against the pygidium. After this point is contacted, A draws the proximal portion of the aedeagus upward. This causes its tip to move ventrally, since the pygidial spine of B acts as a fulcrum, fitting in the ventral trough of the tegmen about midway along the parameres. When the tip of the aedeagus moves downward and forward it comes into contact with B's sternite. When B is female, the sternite resists the downward movement of the aedeagus, as the latter catches in the groove between the marginal sclerite and sternite. On the other hand, if B is male, the groove fails to catch the tip of the aedeagus, which slips freely past. This appears to be due to the combined features of the apical marginal sclerite and the pygidial spine of male B.

When males are probed, dismounting is the only outcome. This is elicited either when a probing male's aedeagus slides past the groove between male B's marginal sclerite and sternite or when its aedeagus contacts that of B. The probing of females, on the other hand, has several possible outcomes, depending upon her receptivity. Immediate insertion of the aedeagus occurs when B has her hind sternite already lowered prior to probing, but when it is not, the prying movement of A's aedeagus may lower it, provided B is a receptive female. If she is not, a male may be unable to insert its genitalia, and will persist in probing until (1) coitus is achieved, (2) he is knocked free of B as a result of her ''frenzied'' scurrying, or (3) until he fatigues (or appears to fatigue).

The hypothesis that sexual recognition by males is chiefly a physical process was tested in the laboratory by altering the structure of the last segment in both sexes with glue. Some evidence was obtained in support of the hypothesis, as the attempt to create a female-like male was partially successful. Males behaved quite differently after mounting and probing altered males than they did when courting normal males. All of the results obtained at first did not seem consistent with the hypothesis, but it was discovered subsequently that consistent results cannot be expected unless the last segment of an altered male is held tightly closed. After this was taken into account, the results were less variable. Some males then mounted and probed altered ones several times in succession before dismounting. Others continued probing for up to 5 minutes.

Physical contact definitely plays an integral part in sexual recognition by males. The important question that remains unanswered seems to be this: when a female holds the hind sternite in closed position as she is mounted and probed by a male, is the response of the male dependent entirely upon physical contact or does he receive some additional stimuli (e.g. chemical) which work in combination with the physical ones? If attempts to modify the structure of the hind sternite of females had not failed completely, a more definite answer to this question might have been possible. Unfortunately, the minute size of the crucial structures makes it impossible to smooth them over with glue or similar substances, like those used to modify the structure of the hind sternite in males. The mass of the applied material inevitably produces a bump which is more of an obstruction to the aedeagus than the groove between a female's hind marginal sclerite and sternite. Other means must be found to smooth over this groove and there must be more tests carried out with females that have an excised male aedeagus implanted in the opening to the abdominal cavity. The small amount of evidence obtained by the latter technique seems to indicate that males may not recognize females by means alternative or additional to the physical ones.

Insertion of Aedeagus and Insemination. After insertion of the aedeagus is initiated the female pygidial spine apparently continues to play a significant role for successful coition. It continues to act as a fulcrum while the male alternately lifts the proximal part of the tegmen and then pushes the aedeagus into the ovipositor tube (fig. 34, 39c). These movements by the male seem to assist insertion by putting pressure against the female's hind sternite to push it downward, and the sheath-like lower part of the ovipositor tube is probably simultaneously pulled away from the fleshy upper portion.

When full insertion of the aedeagus is achieved (fig. 39d), the male's hind sternite is nested in the notch between the tips of the female's elytra, while her pygidial spine rests in the proximal part of the ventral trough of the aedeagus (which faces dorsally in the inserted position). After several minutes the male begins a series of vibrant movements, at which time the middle and hind legs are usually extended laterally. Eversion of the internal sac probably starts with commencement of these movements, because males removed from females during this phase of coition had the internal sac partly everted, protruding from the gonopore. Males removed somewhat later lose the internal sac which is apparently restrained by the spinules around the opening to the bursa.

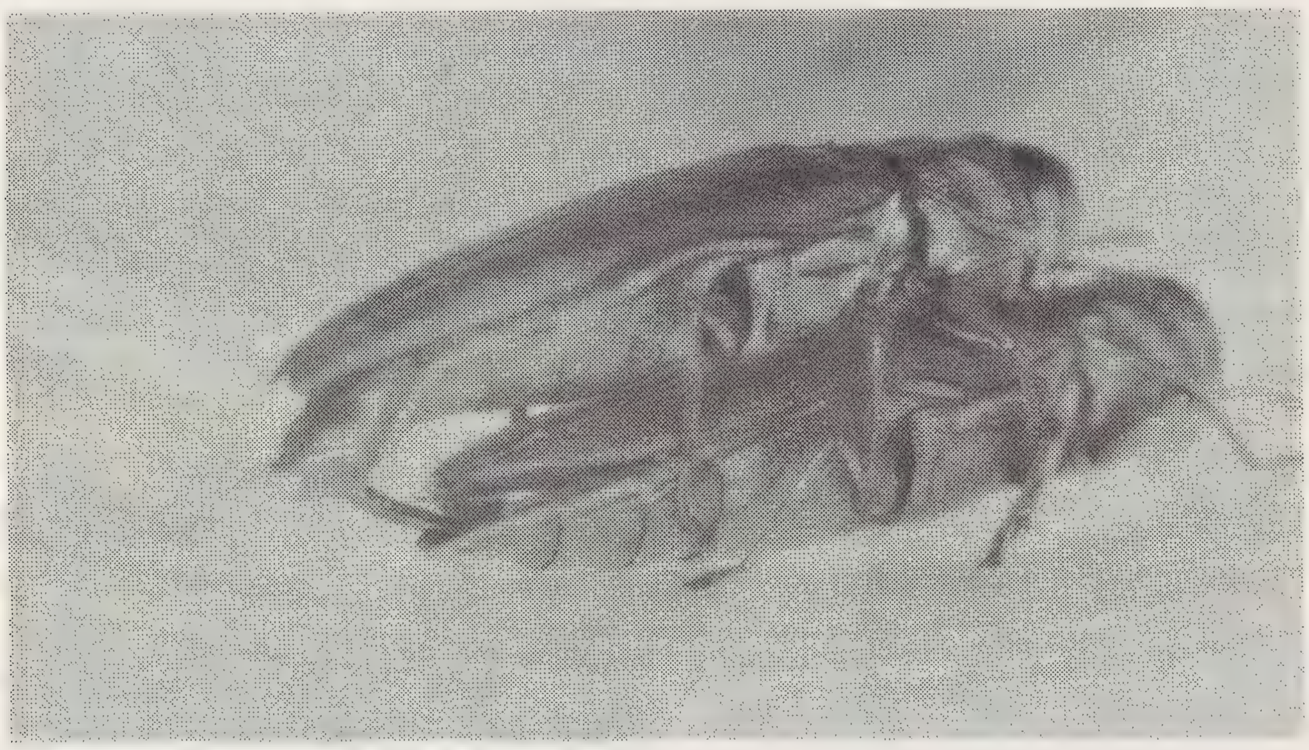

Fig. 34. Mating of an A. anxius ♂ and an A. granulatus liragus ♀. The aedeagus is being pushed into the ovipositor tube (not visible) following the prying of the last sternite away from the pygidium. This downward prying occurs when the male raises the abdomen, which brings the median part of the aedeagus into contact with the pygidial spine of the female, which acts as a fulcrum.

Behavior of Males Under Natural Conditions. Information about Agrilus spp. suggests that they depend upon host selection, at least in part, to bring about the meeting of the sexes. In other words, the kind of site utilized for mating by a particular species depends on many of the same factors which govern the selection of sites for oviposition. Therefore, these are also the factors which prevent interspecific matings from occurring, while making it quite likely that intraspecific pairings do occur.

Bronze Birch and Bronze Poplar Borers. Excepting the host specificity factors, the mating behavior of anxius and g. liragus is similar. For efficiency in making observations, most field work on the mating behavior of these species involved watching individuals which were on windfalls (fig. 35), logs, or logging slash (fig. 36). It is fairly safe to assume that they do not behave very differently on these hosts than on upright ones.

The males of g. liragus and anxius move along the stems of their hosts, usually remaining still for only brief but frequent interludes. On very warm days, the movements of these beetles are rather rapid and the hesitations are very brief, so that they move rather continuously with a jerky motion. On cooler days they remain stationary for rather long periods, and are not conspicuous. These insects are not active at temperatures below 70° F (Barter 1957, 1965).

When any arthropod passes within a foot or so of these Agrilus males, the males approach the former. If the other animal, in turn, approaches them aggressively, such as was observed with ants and males of a larger buprestid, Chrysobothris sp., the Agrilus male responds by releasing its grip on the host and falling free of it. However, if the other arthropod is moving away from the Agrilus, the latter pursues. In one instance a g. liragus male was seen following a Dicerca (another buprestid), and upon overtaking the latter, the g. liragus male actually scurried part way up onto the elytra of this much larger insect.

When two anxius or g. liragus males approach each other, they usually do so more gradually, at least if each has detected the other, which usually is the case. After the males stand facing each other from a distance of one to several inches, one of them quickly approaches and mounts the other. Such homosexual encounters occur very frequently in nature, much more frequently than heterosexual ones. They may have a special significance, particularly for anxius and g. liragus.

Homosexual encounters seem to have a survival value that is real. A. anxius and g. liragus males exhibit a sort of quasi-territorialism on their hosts. After a male mounts and probes another, he usually flies or walks to a different part of the host. These encounters between males seem to have an interesting uniqueness in that it is the aggressive male that is usually repelled. There is nothing to indicate that the aggressor can be repelled by anything short of mounting and probing. The seemingly inefficient means by which the males of these Agrilus recognize each other may be important in keeping them spatially separated. This quasi-territorialism among males may serve to increase the probability of occurrence of heterosexual encounters.

The beneficial effects of homosexual encounters may not be derived without some cost to the sexual responsiveness of the aggressive male. During laboratory studies of behavior it was discovered that if males are removed from females just after completing the sexual recognition phase of courtship and are immediately released again, they often mount the next individual they encounter (either sex). The sexuality of males is definitely enhanced when they mount and probe females, and it is apparently not greatly diminished by artificial termination of courtship. However, males whose sexual responsiveness has been enhanced in this way, seem to lose it after a short sequence of homosexual encounters. Perhaps the decrease in sexual aggressiveness occurs as an integral part of the reaction which causes an aggressive male to move away from the one he has mounted.

Fig. 35. Populus tremuloides windfall, typical of those where the adult behavior of Agrilus granulatus liragus was observed.

Fig. 36. Betula papyrifera logging slash, a typical observation site for the studies of the adult behavior of Agrilus anxius.

Apparently, there is some sort of threshold which must be reached before courtship is elicited in males, and when that threshold has been reached or exceeded, males court immediately upon encountering other individuals. All males on their hosts under natural conditions seem to have high sexual responsiveness. This indicates that factors associated with their attraction to mating sites and their pre-courtship behavior may induce this responsiveness.

During their vigil on the host, *anxius* and *g. liragus* males are often observed repeatedly exserting the aedeagus. This behavior is also exhibited in the laboratory by males not on their hosts, and it seems to occur well in advance of the attainment of the mating threshold. It could be a protagonistic aspect in a part of the male behavioral repertoire that is somewhat self-regulated as a balance between protagonistic and antagonistic aspects. The existence of this kind of behavioral balance has been demonstrated in other groups of insects (see Kennedy and Booth, 1963; Graham, 1959, 1961).

Little has been established concerning the extent to which the energy of females, once they have reached the host, is spent in activities which lead to encounters with males. Most field observations seem to indicate that they are rather passive. On the other hand, laboratory studies of mating indicate that females may court males. On a number of occasions, virgin *g. liragus* females mounted males and displayed many of the actions typically manifest by males in courtship. In some cases the ovipositor was even exserted. Virgin *anxius* females never showed such a striking ''maleness'', but occasionally they moved part way up onto the elytra of males and flailed the antennae in the manner of courting males. Whether or not virgin females would show the same sort of response to other females is not known. No such behavior was ever observed in the field, and must happen only rarely, if at all. Moreover, under natural conditions, males seem to most readily mount individuals which turn away from them. It is difficult to reconcile this with active courtship by females, unless it is natural for the sexual aggressiveness of females to be subordinated by that of advancing males, with females terminating their courtship by turning away from males.

According to Barter (1965) *g. liragus* males ''actively seek or ambush non-ovipositing females.'' He says that ovipositing females are unattractive to males, but this does not appear to be an entirely accurate statement. Barter observed mating less frequently between 1:00 and 4:00 PM, the peak hours of oviposition. This alone does not show that ovipositing females are unattractive to males, however. Males simply do not encounter ovipositing females frequently. Females ovipositing on logs are found along the sides of the logs on days when the males orient more to the upper surface. Ovipositing females are, therefore, usually not within the line of sight of males.

Because females are motionless while eggs are being deposited, males are not likely to detect them then. However, ovipositing females are approached by males which detect them moving between egg deposition sites. One ovipositing *g. liragus* female under observation was approached by two males. After moving away from the first male, she was encountered by the second. Although she also moved away from the latter, he overtook her and mounted. The female stopped moving only after the male had inserted the aedeagus, after which copulation proceeded normally. Therefore, ovipositing females are not unattractive *per se*, although they may be rather unreceptive to courting males.

Laboratory observations indicate that females courted after having recently mated are particularly unreceptive. When females are totally unreceptive, courting males are usually unable to insert the aedeagus. It appears that total unreceptiveness occurs only after insemination occurs. When males are removed from females during the course of mating and prior to insemination, the females are usually receptive to the next male to court them.

The Aspen Root Girdler. Although *g*. *liragus* and *anxius* are provided with a means for meeting of the sexes which apparently depends upon odors coming from bio-chemical degradation of the host, *horni* mating is brought about through more subtle means. *A*. *horni* males are apparently able to select hosts of a favorable physiognomy and in such ecological situations that the chances for encounters with females are enhanced, but it hardly seems as certain a means as that common to *anxius* and *g*. *liragus*. There is a possibility that *horni* males or females emit air-borne sex attractants. There is no evidence to suggest that this is the case, however. *A*. *horni* males merely seem to orient to poplar suckers which females are likely to land upon. They sit on the sucker stems, facing upward, and their position usually ranges from near the ground to near the point where the sucker's lowest side branches are produced, a height of about one to three feet. The males stay in nearly the same position for periods averaging about 15 minutes, during that spell usually moving only when another arthropod moves near it on the stem. After such a period, they move upward and out onto the leaves to feed for one to several minutes before resuming their vigil on the stem. One male remained on the same sucker for more than 2 1/2 hours, but this may be an exceptionally long stay.

The entire *horni* courtship and copulation was observed only once in the field. In that case, as the female came down the sucker stem and neared the stationary male, he, in turn, approached her. The female then flew, but landed again on the foliage of the same sucker, while the male moved rapidly to the base of the sucker and turned upward. The female came down the stem again, and when she was approached by the male she turned upward. The male moved up quickly from below and mounted. After they had been in copulo for about 15 minutes, the female crawled up the stem and onto a leaf where the male dismounted. In one other instance in the field, the last part of *horni* copulation was seen, and it terminated just as in the preceding one. In each case, the female flew to another sucker as soon as the male dismounted.

There is an interesting parallel between these field observations and laboratory observations on *horni* copulation. In the laboratory, too, the males remained mounted after the females began moving around. In one instance a copulating female which had remained still for 10 minutes, ran about in the petri dish for 24 minutes with the male remaining mounted. In another case, the female remained placid for 17 minutes, but ran about for the remainder of the mating period, which totalled 21 minutes. In a field cage (fig 37), a copulating female which fell from an aspen sucker with the male still mounted, ran about on the ground for 40 minutes before the male was dislodged. The tegmen was partially to fully inserted during the entire 40 minutes. Several times the female seemed to orient towards debris which she could pass beneath, but which would not allow the male to pass freely. It is difficult to believe that the behavioral repertoire of *horni* females could include such a specialized facet for dislodging males. After it had occurred several times, however, the possibility seemed less remote.

The males of *anxius* and *g*. *liragus* do not usually remain mounted long after the females begin moving about. Barter (1957, 1965) found that the av-

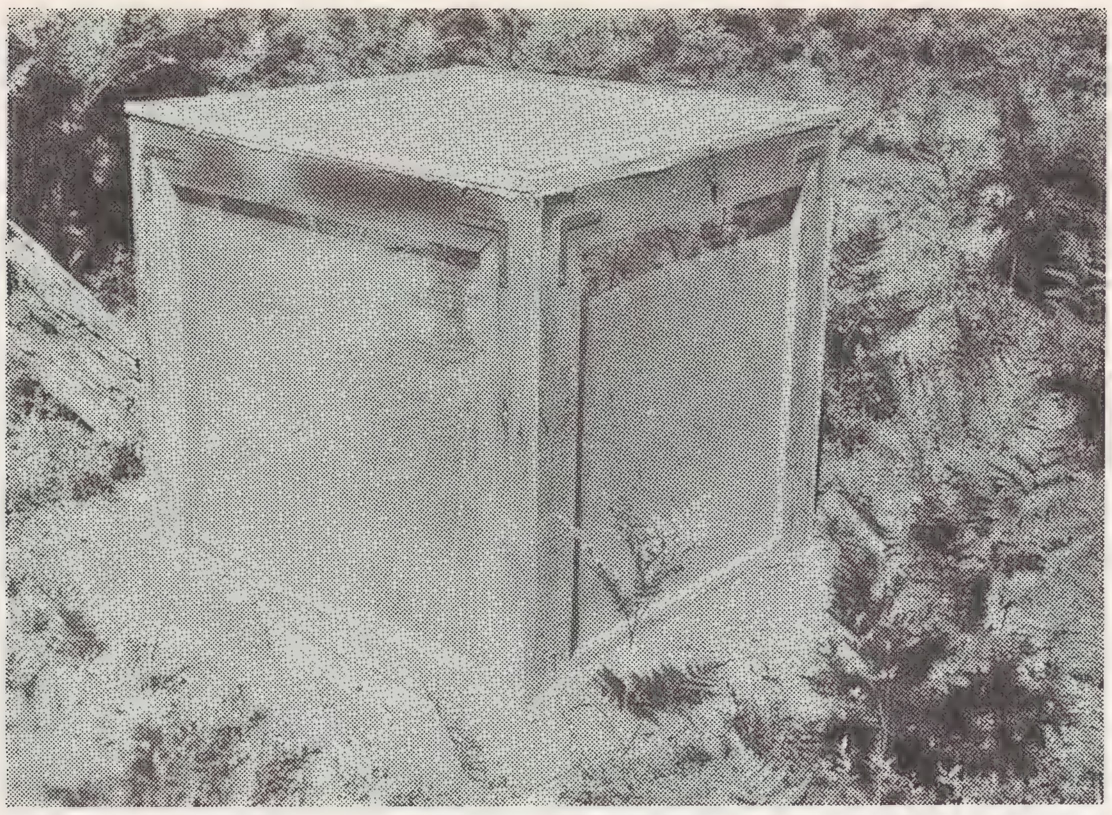

Fig. 37. One of the field cages where some observations on Agrilus horni adults were made. Note that these observations are not those designated in the text as field observations; the latter, comprising the majority discussed, refer to observations on beetles not in captivity.

erage time elapsed in copulo was 7 minutes for anxius and 5 minutes for g. liragus. He says the maximum observed for anxius was 23 minutes.

FEMALE ACCEPTANCE OF MALES. Other species differences in mating behavior were discovered primarily through attempts to obtain interspecific crosses in the laboratory. These experiments showed that the females of Agrilus horni will not mate with g. liragus males. In 43 recorded attempts to obtain this cross, none was successful, as the g. liragus males could not insert their genitalia. Often, these males would remain mounted for extended periods, up to 5 minutes or more, continually probing the hind segment of the horni female.

In 29 recorded attempts to cross anxius females with g. liragus males, only 4 led to copulation. A. pensus females, on the other hand, appear to be receptive to g. liragus males. They are also receptive to anxius males, but may not be receptive to horni males. In a number of attempts to pair horni males and pensus females, the latter usually did not seem to be receptive, and copulation resulted only twice. In one of those cases the pensus female did not seem entirely receptive. The difficulties encountered with the survival of pensus adults abbreviated the testing of this interspecific pairing, and left us with inconclusive results. A. granulatus liragus females are promiscuous, accepting males of any of the four species involved in these tests.

When a male mounts a female, he thrusts his head and prothorax forward and flutters the antennae over her head and the base of her pronotum (fig. 38)[1], and sometimes they are simultaneously drawn back rapidly making a long stroke over the lateral parts of the pronotum (fig. 39). At the same time males palpate the female's pronotum near the depression lying just anterior to the scutellum. Sometimes, males perform these antennating and palpating move-

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[1] The antennal movements during courtship appear to be the same as those occurring later. Because it is extremely difficult to get the beetles into proper position for photographing during courtship, I am forced to use photographs taken during copulation.

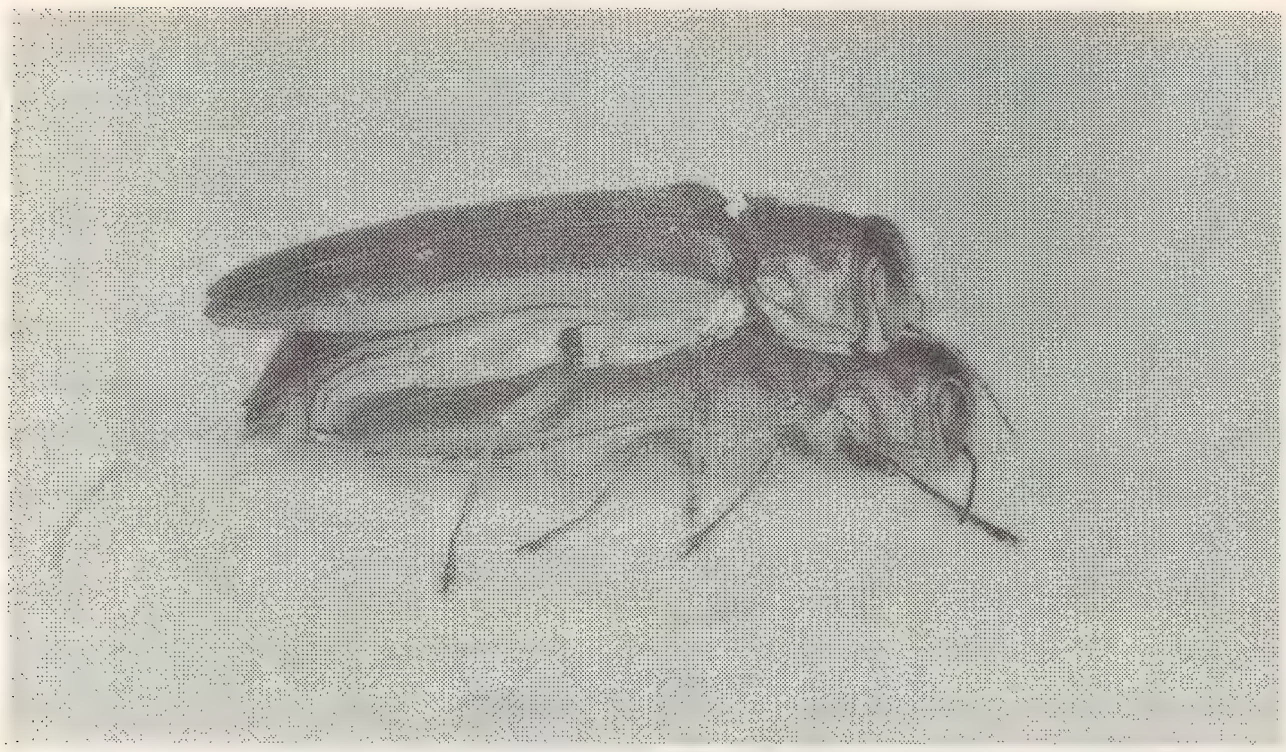

Fig. 38. Position of the antennae at one point during "fluttering" by an Agrilus anxius ♂. The antennal fluttering observed during courtship seems to be the same as that occurring during copulation. Compare the position of the antennae with the positions shown in figure 39.

ments(collectively, hereafter antennation) prior to probing with the aedeagus, and when insertion does not occur quickly, they are repeated during the probing phase. Antennation also occurs as the aedeagus is being inserted; it is repeated occasionally until the male starts the vibrant movements thought to attend insemination, and is performed following insemination as the aedeagus is being withdrawn.

No incontestable evidence could be found regarding the nature of the intersexual communication which leads to females accepting or rejecting males of a particular species. However, it does seem to have something to do with antennation by courting males.

If a female begins to move during insertion and the earlier phases of copulation, antennation appears to tranquilize her again. Exceptions occur in some interspecific pairings, or when females are unreceptive as a result of recent copulation. In these cases females usually run about despite antennation by males. Males may have difficulty withdrawing the internal sac and penis while the female is moving. This may be the reason for the occurrence of antennation as the aedeagus is withdrawn, and the selective advantage which favored the development of this behavior may stem from the reduction in incidence of injury to the male genitalia.

A comparison of the courtship behavior of anxius, g. liragus, and horni yielded some data concerning the basis for the unreceptivity of horni and anxius females to g. liragus males. During antennation the males of horni and anxius usually contact the head and pronotum of the female. A. g. liragus males, on the other hand, often do not touch the female with the antennae during courtship, and when they do, seem to do so very lightly. However, there seems to be too much intraspecific variation for this alone to account for the entire lack of receptivity of horni females for g. liragus males. Even when horni males seem to antennate very lightly, they are accepted by conspecific females, and the few times when g. liragus males appeared to antennate like horni males they still failed to elicit receptivity in horni females.

Examination of the scape and the antennal sockets of these insects at high

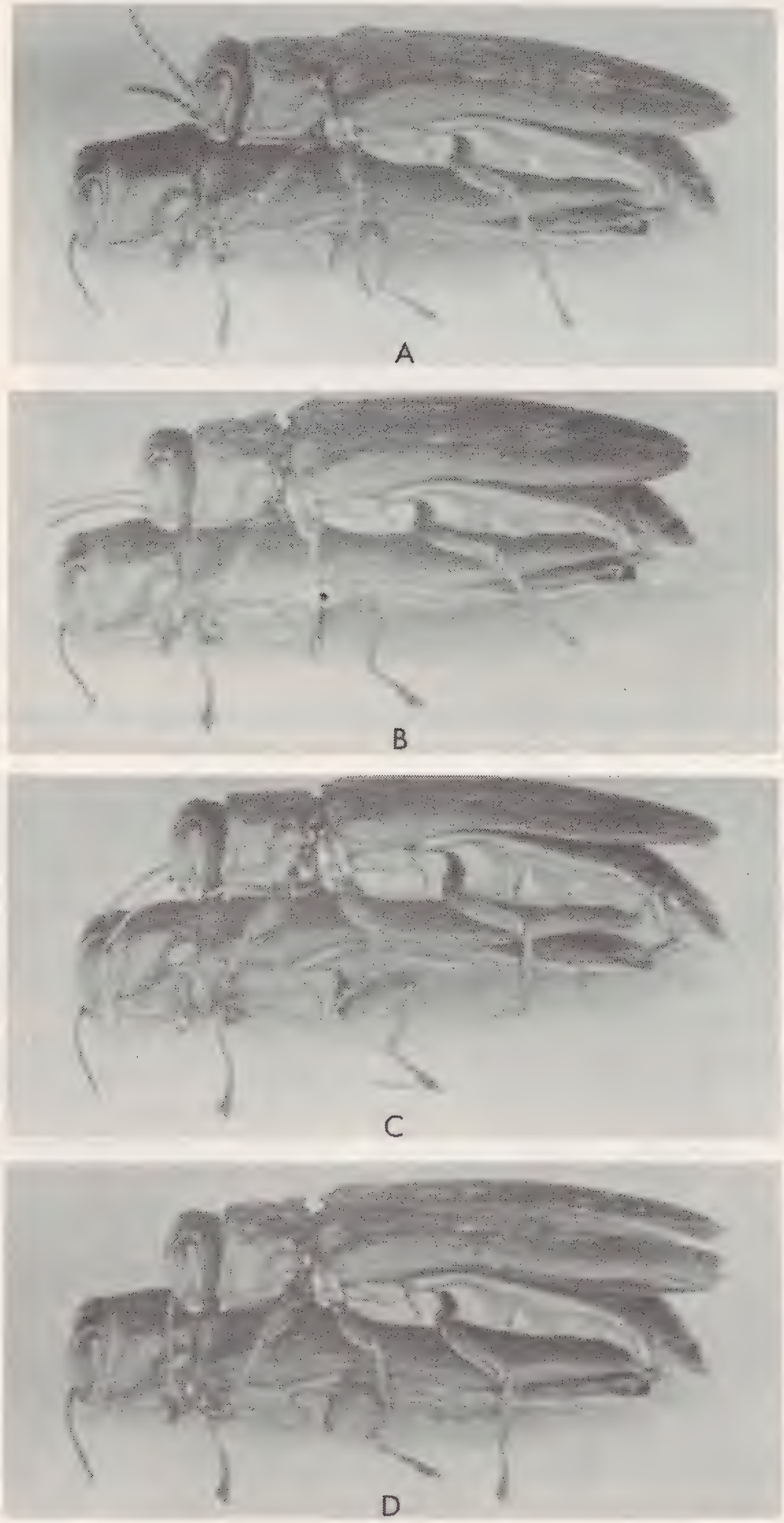

Fig. 39. Positions of the antennae during the stroking movements of males (here *Agrilus granulatus liragus*) in copulo or courtship, arranged sequentially: (A) being moved forward, (B) maximum anterior extension, (C) beginning of backward stroke, and (D) finish of backward stroke.

power (90X) indicates a remote possibility for high frequency vibrations or slight sounds being produced by some of the movements involved in antennation. The undersides of the scapes (reposed) are flattened and striate. Similar striations are found on the lateral rim of the antennal sockets and on the part of the front between the antennal sockets and the eyes (fig. 40). Movement of the scape over the striations on the antennal socket and front, as occurs during antennation, must produce some friction and thereby vibrations or sounds. The question is whether or not such vibrations or sounds could be intense enough to serve in communication. When the head is thrust forward during antennation (fig. 39, above), the increase in hydrostatic pressure should be transmitted to the antennae. This, in turn, may increase the friction between the scape and the striate surfaces on the antennal sockets and front.

The frontal striations are definitely strongest in horni, weakest in g. liragus, and of intermediate strength in anxius. Consequently, any sound or vibration produced might be somewhat species specific. In comparing the structures with other species in the anxius group, we found that some of them, vittaticollis for example, have even stronger frontal striations than horni. Perhaps these species should be studied first in an effort to determine the significance of the striations.

Stridulation

The possibility that other auditory, vibrational, or chemo-tactic communications might be responsible for species discrimination by females cannot be discounted. Both sexes do produce stridulatory sounds that have been recorded. The method of stridulation is one apparently peculiar to Agrilus, and has been reported for A. solieri Castelnau & Gory and A. cinctus Olivier (neither sp. in anxius group) by Schaefer (1949). It involves a rapid rotation of the head in its prothoracic socket. Males of anxius, pensus, g. liragus, or horni have not been seen making these movements during courtship. Moreover, the

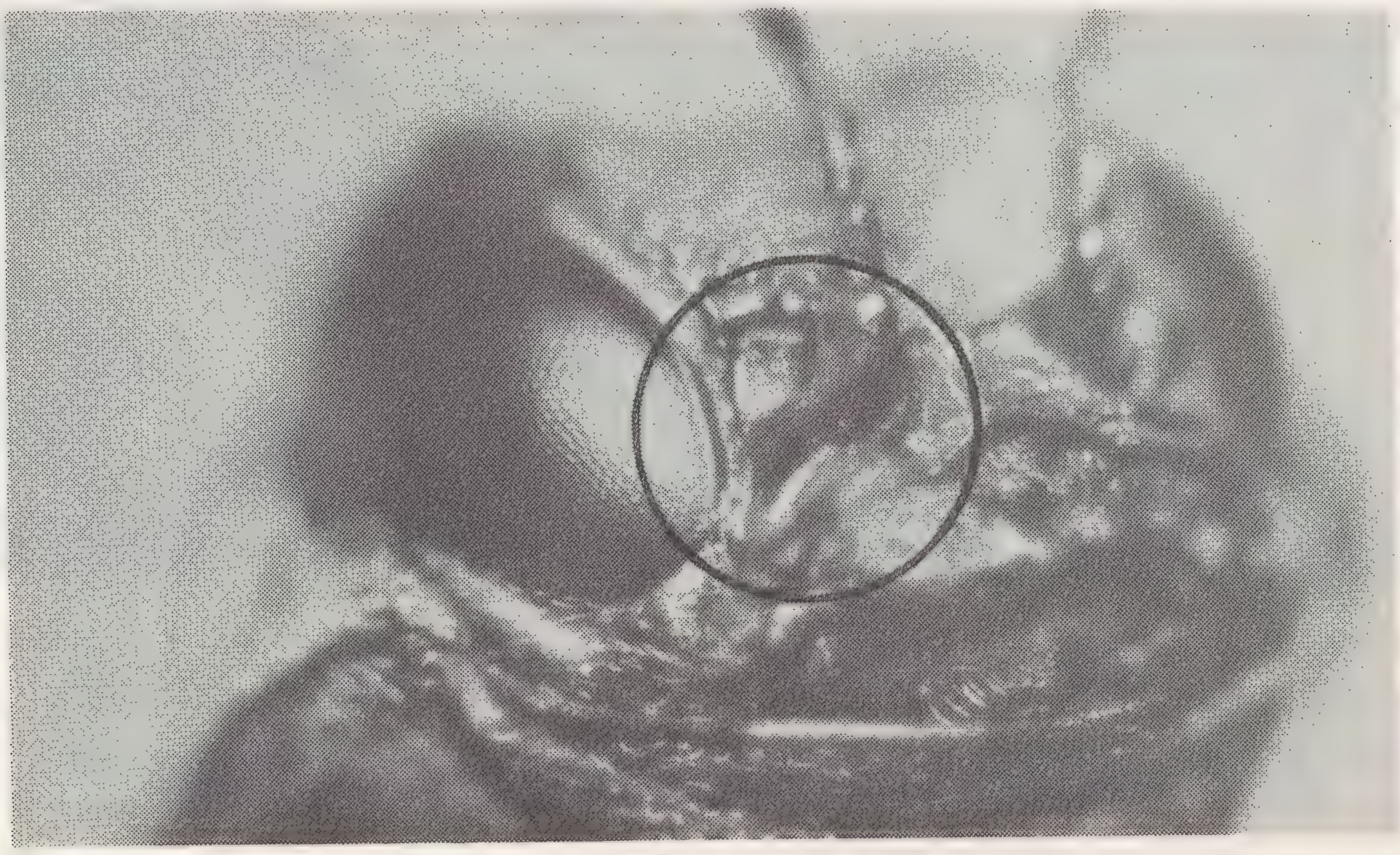

Fig. 40. Frontal view of Agrilus vittaticollis ♂ (X42); within the circle are the striate areas between the antennal socket and the eye and on the underside of the scape. The striations are coarser in this species than in horni, anxius, pensus, or g. liragus.

sounds produced by these stridulations seem to have no connection with female recognition of males in these species. The only time during courtship that the head is involved in pronounced movements is during antennation, after it has been thrust out of its prothoracic socket. The only situations in which stridulation has been noticed are ones which would indicate that the noises produced could be classified as stress sounds.

In stridulating these beetles tilt the head slightly forward at the top. This apparently brings the genal ridges[1] (the carinae at the lower edges of the genae; fig. 41) into position to contact the prosternal lobe. The genal ridges act as the scrapers, while the fine imbrications on the prosternal lobe serve as the file (fig. 42). The latitude of the rotational movements of the head during stridulation is quite small, in the neighborhood of a millimeter. Because of their rapidity it was difficult to count the movements, but there are approximately 5 head movements per second to each side of the center position. This agrees roughly with audiospectrographs (fig. 43) which show that the file is contacted about 10 times per second. The sounds produced are very soft. Consequently, it was rather difficult to record them.

As one might expect of sounds that are really only stress-induced, there is no indication that these Agrilus sounds are species-specific. These beetles probably do not produce other kinds of sounds with this same stridulatory apparatus. As previously noted, stridulation has not been observed in a situation that would definitely indicate that it was not stress-induced. There were a few indications that it may elicit repulsion of individuals that contact stridulating beetles. Alexander, Moore, and Woodruff(1963) suggest that, inasmuch as the sounds of Coleoptera are usually too soft to function at long distances, they may function in several fashions among adults in close proximity. The stridu-

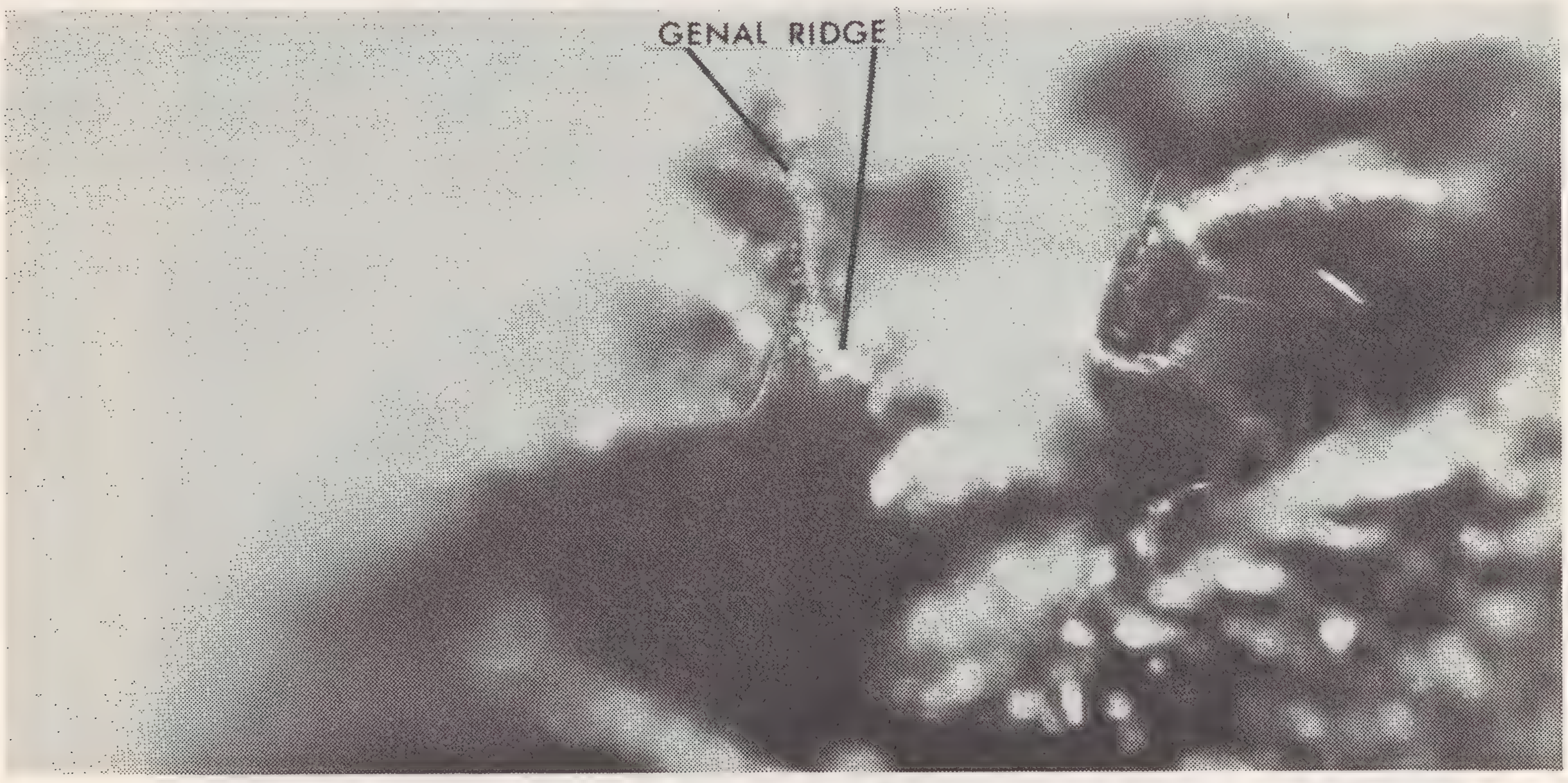

Fig. 41. Postero-ventral view of the head of an Agrilus horni ♀, showing the genal ridge (X109). Note the fine striations which are barely visible at one point near the posterior end of the ridge; they may be important in stridulation, but the sharp posterior portion of the ridge's outer edge may also contact the prosternal lobe (fig. 42).

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[1] Mr. G. B. Vogt, U. S. Dept. Agr., A.R.S., Entomology Research Division, Washington, D.C. believes that "genal ridge" is the best possible term for this structure (personal communication).

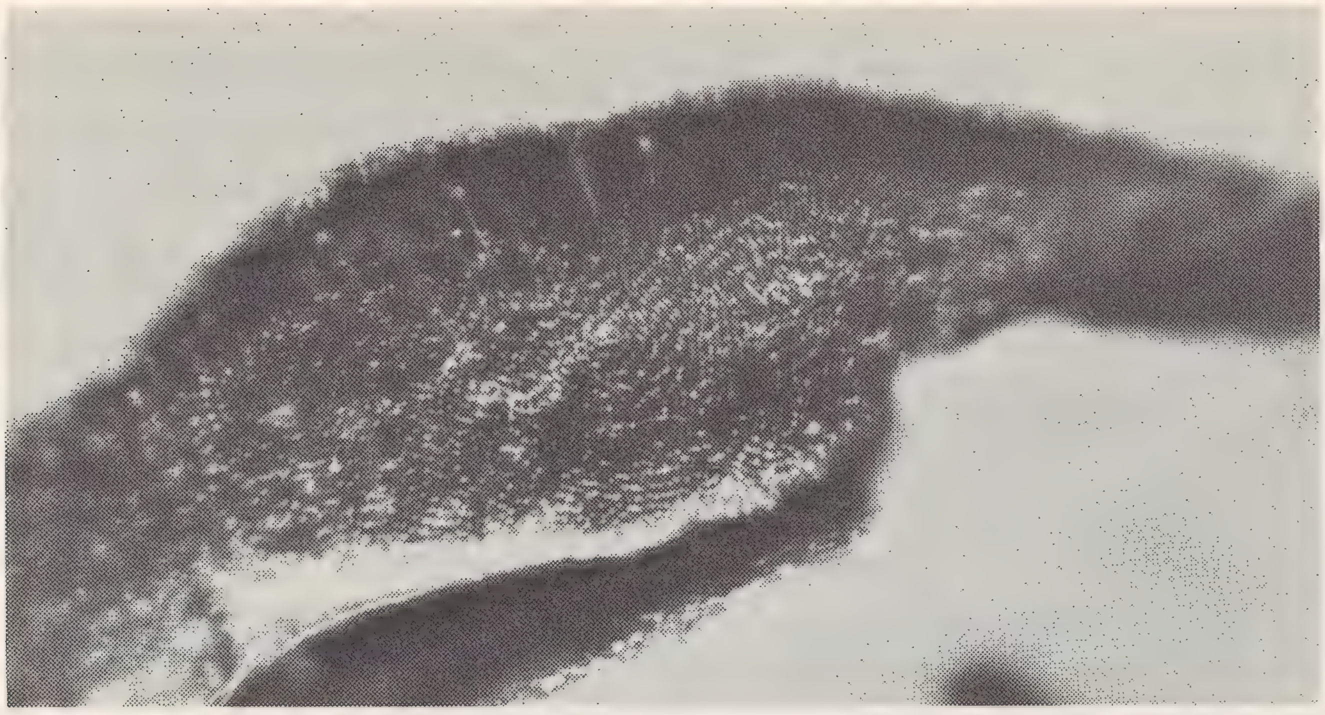

Fig. 42. Finely imbricate interior surface (head is excised) of the right half of the prosternal lobe of an Agrilus horni ♀ (X82).

latory apparatus of the species which were examined thoroughly (anxius, g. liragus, pensus, and horni) was not sexually dimorphic, and recordings indicate that there is no sexual difference in the sounds produced. They do not appear to be directly associated with courtship. Although unreceptive females may occasionally stridulate, their stridulation does not seem to have any effect upon courting males. In homosexual encounters, a sexually aggressive male is usually repulsed only after he mounts and probes the other, and stridulation does not seem to be involved. Nevertheless, stridulation may function in some other situations to prevent over-congregation of males or females, or they may serve to repel individuals of unrelated Agrilus species which may live on the same host. These stridulations should evolve toward nonspecificity in the eliciting stimulus (Alexander, et al., 1963). It is, therefore, difficult, if not downright impossible, to assess their significance by studying them under artificial conditions. On the other hand, as these Agrilus stridulations cannot be heard, except through amplification or by placing the insects next to the ear, and because the movements cannot be seen at distances of more than a foot or so, anyone endeavoring to determine their real function under natural conditions, will, to say the least, be faced with a real challenge.

EVOLUTION

Phylogeny

When our work on Agrilus was initiated, we had not pondered seriously enough the possibility that anxius, pensus, horni, and g. liragus are not all closely related. It seemed that the important questions to be answered concerned isolating mechanisms and clues to how these species evolved from a hypothesized common ancestor. Because of this improper assessment, more species than originally anticipated will be brought into discussions about phylogeny.

THEORETIC BASES. It is quite usual to regard some characters as more reliable than others as indicators of phyletic relationships. Nevertheless, we

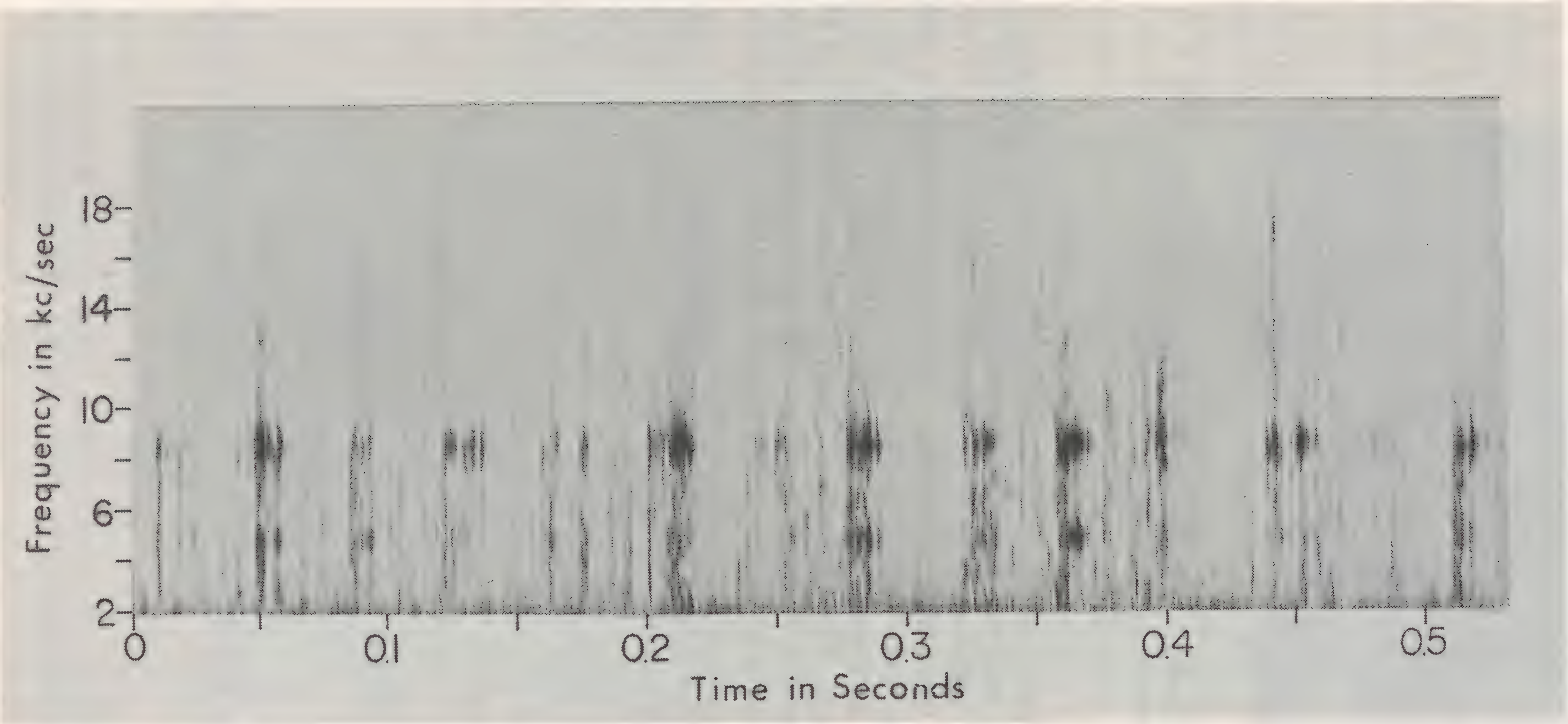

Fig. 43. Audiospectrograph of stridulatory sounds of an Agrilus granulatus liragus ♂. The tape recording was made with a Magnecord Model PT63A2HZ recorder, a Magnecord Model PT63-J amplifier, and an American Model D33-A microphone, at a tape speed of 15 inches per second. Two persons were required for making recordings. One held the beetles near the microphone and gave signals to the other, who operated the recorder. This allowed the microphone to be placed at a distance from the recorder, minimizing interference from sounds associated with operation of the recorder. The audiospectrograph was made with a Kay Electric Company Vibrilyzer, with signals fed in by the amplifier mentioned above, at 1/4 the tape speed of the original recording. Two runs were used to make the markings as dark as possible. The vibrilyzer settings were: mark level gain 8. 0, wide band width, shape flat, high gear, and low motor speed.

shall set forth the assumptions concerning those we use, and give our reasons for not considering others to have the value accorded them by other students.

Let it be made clear at the onset, that we do not regard any characters as being "nonadaptive." Many systematists have used the term nonadaptive in reference to stabilized characters, while referring to those subject to much variation as "adaptive." The irrationality of the idea of adaptivity and nonadaptive is discussed by Dobzhansky (1956), who maintains that all traits, or at least the vast majority of them, are adaptive or have been adaptive at some time in the history of their development. To be sure, some traits are more stable than others, but their stability should relate to the kinds of functions rather than to the existence of functions versus the lack of them.

In many cases it is difficult to perceive functions for some seemingly trivial traits, but this is a poor reason for assuming they do not exist. So it is with the pygidial spine of species in the *Agrilus anxius* group. Without searching for its function, one might take what seems to be the prevailing attitude in such cases--that its stability indicates that there is no selection against it, probably because it is of no great disadvantage to its possessor. Quite to the contrary, it seems that the stability of the pygidial spine stems from its importance in the process of sexual recognition. Any large changes in the form or size of the pygidial spine calls for corresponding changes in the form of the male aedeagus and other structures. In genetic terms, it probably owes its stability to an association with pleiotropic genes whose total influence on the developmental system is spared extensive changes through the moderating influences of homeostasis or coadaptation (see Dobzhansky, 1956).

The pygidial spine probably has at least as much stability as characters ordinarily given tribal or generic value in other insect groups. Perhaps Obenberger was the one taxonomist who should have had sufficient worldwide familiarity with *Agrilus* to recognize this, but he was convinced of the impossibility of even dividing *Agrilus* into acceptable subgenera (see Obenberger, 1959). What Obenberger (1957) implies is that, to be valid, each proposed subgenus must have as its basis a single character which occurs among no species of other groups. If any *Agrilus* character could meet this absurd requirement, it would probably be the pygidial spine. Obenberger (1957) denies this possibility because (1) a pygidial spine is found in the Palearctic forms *Agrilus guerini* Lacordaire, *A. fleischeri* Obenberger, and *A. ater* L., but is absent in an alleged intimate ally, *A. suensoni* Obenberger; (2) its presence among about 30 African species makes it self-evident that it occurs among entirely unrelated groups.

To counter the first point one need only ask what criteria he uses to ally *suensoni* with *ater* and the rest. He offers none, and almost any should be more subject to convergence than the pygidial spine is to total disappearance. Obenberger's second point is even more indefensible because the presence of the spine among African species cannot, in itself, demonstrate that it has arisen repeatedly. There is no *á priori* reason for believing that even the Ethiopian species he mentions do not share common ancestry with Palearctic ones. After all, the Palearctic region does extend into northern Africa.

INTERPRETATION. Fisher (1928) has given the form of the tarsal claws precedence over the pygidial spine in his classification. As a result, three species which are here placed in the anxius group are classified quite apart from it by Fisher. These are *Agrilus ruficollis*, *A. champlaini* Frost, and *A. browni* (= *lateralis*, *sensu* Fisher [1928]; see p. 6). The bifid claws of these species have the inner lobes bent toward each other. This trait appears to be the only one which they have in common with the species Fisher places them near. The pygidial spine, the marginal sclerite of the hind segment, and the general form of these insects links them with species in the *anxius* group.

On the other hand, *ruficollis*, *browni*, and *champlaini* have more in common than just similar tarsal claws. They resemble each other in the structure of the pronotum, elytra, and male or female genetalia. In addition, *ruficollis* and *browni* are similar in coloration. Their hosts are not closely related, but the larval habits of all three species are somewhat alike. The larvae of *ruficollis* bore in the stems of brambles (*Rubus* spp.). During the early stages of development they often (cf Smith, 1892) form galls by making a tight spiral in the phloem, while late-instar larvae move rather directly up and down the pith. *A. champlaini* forms galls on ironwood (*Ostrya virginia*) and blue beech (*Carpinus caroliniana*), but the late-instar larvae spiral mostly in the wood within the gall which forms as the result of the phloem blockage caused by the gallery of the early instars. Fisher (1922) reared *browni* from bayberry (*Myrica pensylvanica*), and Knull (1922, 1950) says *Myrica asplenifolia* is also a host. The *browni* larvae make no galls. According to Fisher (1922), after passing the winter in the roots, the *browni* larvae spiral upward in the limbs for a considerable distance before they reach maturity.

The number and variety of similarities between *ruficollis*, *browni*, and *champlaini* makes it unlikely that they could all be convergent. However, these species differ in ways that seem to push their divergence to a rather remote era. For example, it does not seem likely that a species living on *Ostrya* and *Carpinus* could be intimately allied with species whose hosts are *Rubus* spp. or *Myrica* spp. Consequently, in figure 44, *champlaini* is shown as also having remote connections with species that live on Fagaceae, which includes *Agrilus bilineatus*, *A. acutipennis* Mannerheim, and a number of other forms. While *champlaini* might instead be related to the line represented by *anxius* and its allies, it appears to resemble *bilineatus* and related species in a greater number of minor respects. For instance, the latter have the inner lobes of the tarsal claws turned inward, although to a lesser extent than does *champlaini*.

Allies of horni. *A. browni* seems to be more closely related to *horni* than to *ruficollis* (fig. 44). While its tarsal claws are like those of *ruficollis*, *browni* resembles *horni* in having the vertex less strongly impressed, the front flattened, and the marginal sclerites of the abdomen clothed with white pubescence. The *browni* aedeagus is intermediate in form to those of *ruficollis* and *horni*, but *browni* has a trace of the prehumeral carinae, which are completely lacking in *ruficollis*.

While the eggs of *ruficollis* are placed at the axils of the branches (Hutchings, 1922b) or leaves (Smith, 1891) of its hosts, those of *browni* and *horni* are placed at the bases of the host plants. The larval habits of *browni* and *horni* are very similar (excluding host differences). In each case the larvae bore into the roots and over-winter there. The only difference is that *horni* bores farther out into the root and spirals back to the stem, while *browni* spirals mostly in the branches. The early-instar *ruficollis* larvae, on the other hand, over-winter in the stem and probably spiral only during the time prior to this initial over-wintering period.

Agrilus vittaticollis has the vertex strongly impressed as in *ruficollis*. Fisher (1928) says *vittaticollis* is allied with *benjamini* Fisher and *audax* Horn. The host of *benjamini* is unknown, but *audax* infests the upper branches of *Ulmus*

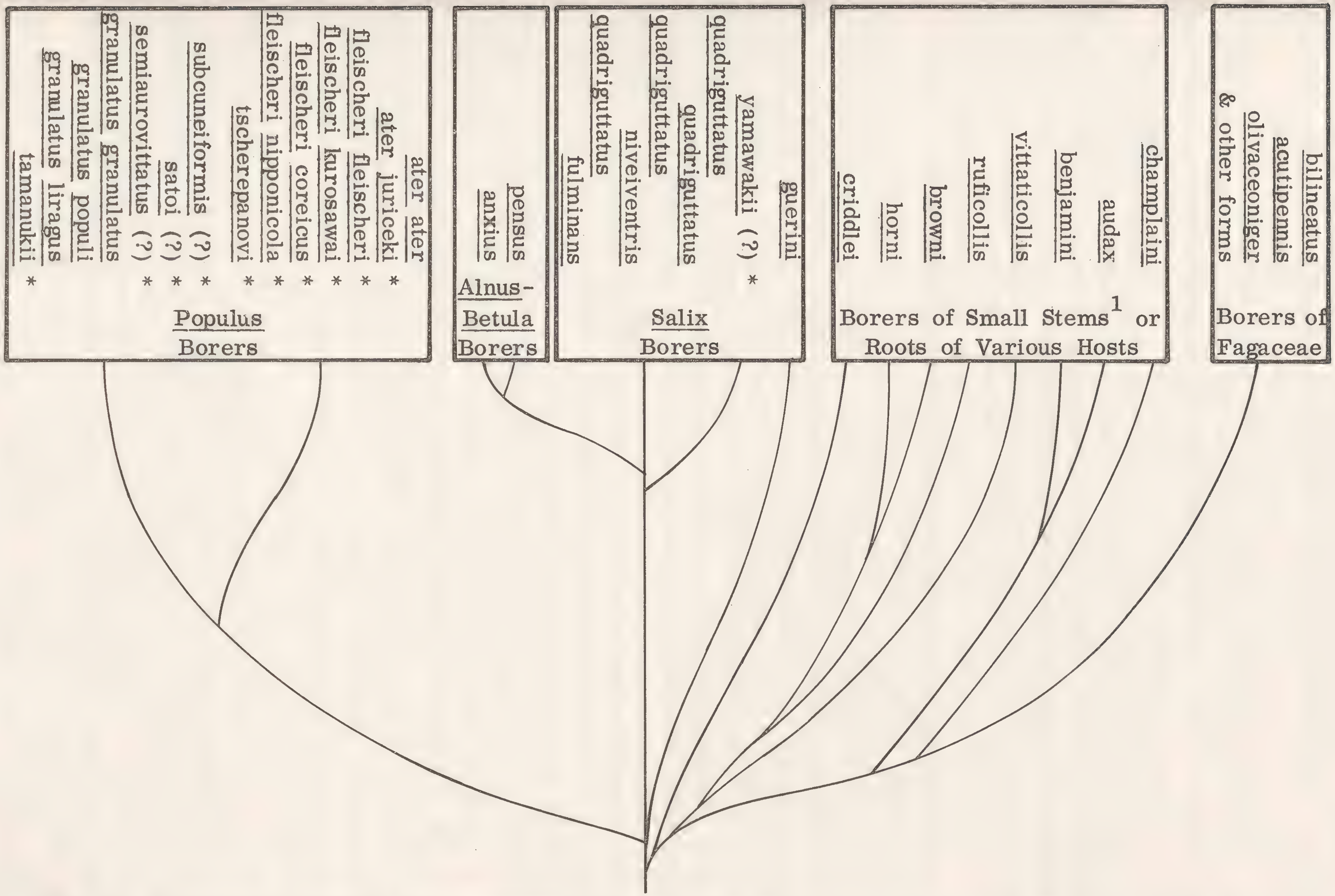

Fig. 44. Hypothetical phyletic tree for some of the described Nearctic and Palearctic forms placed in the *Agrilus anxius* group. The names of taxa of which the authors have seen no specimens are marked with an asterisk. A question mark follows the names of those species for which the designated host specificity is uncertain.

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[1] Also includes gall-making species.

rubra (Knull, 1934). *A. vittaticollis*, however, has a root boring habit quite like that of *horni*, but in its morphology *vittaticollis* bears more similarity to *ruficollis*. Hence, *vittaticollis* is shown (fig. 44) as sharing common ancestry with *ruficollis*, *browni*, and *horni*, but splitting from them before they diverged from each other.

Without exception, *horni* has always been classified as a close ally of *anxius*, on the basis of coloration, the structure of the claws, and the form of the prehumeral carinae. The superficial resemblance of these species is, in fact, so close that without a knowledge of their biology this alliance would seem most probable. It is almost axiomatic that coloration is an unreliable indicator of phyletic relationships. The amount of variation which the prehumeral carinae show throughout the genus, and indeed their complete absence in numerous species, even within the *anxius* group, suggests that they are also unreliable and should be used for classification only with particular caution. The morphology of the tarsal claws appears to be of a similar nature. Nothing more than wild speculations could be offered for explaining why these characters should be variable among species, but relatively constant within. Nevertheless, there probably are sound and logical reasons for it being so.

Probably the most significant morphological features which appear to link *horni* with *browni*, rather than *anxius*, are found in the structure of the male and female genetalia. In *browni* and *horni*, the ovipositor is half as long as that of *anxius* (relative to total body size). In correspondence with the female genetalia, the aedeagus in *browni* and *horni* is shorter than that of *anxius*.

There are a number of other minor characters which seem to separate *horni* from *anxius*, *g. liragus*, or *pensus* and show its relationship to *browni*. (1) In *horni* and *browni* the marginal sclerites of all abdominal segments, except the last, tend to be rather densely pubescent, but in *anxius*, *g. liragus*, or *pensus* the second marginal sclerite tends to be glabrous. (2) The striations on the antennal scape and on the front, between the antennal socket and eye, are nearly as strong in *horni* as in *browni*, while they are weaker in *anxius* and, particularly, *g. liragus*. (3) The elytra of *horni* and *browni* tend to be evenly sculptured and rather evenly clothed with pubescence that is uniformly short. Those of *anxius*, *g. liragus*, and *pensus* are not sculptured as evenly, having a longitudinal costa and a depression mesad of the costa and between the basal third and apical half of the disc. Frequently in *g. liragus*, and less often in *anxius* and *pensus*, this depression is pruinose. The hairs on the elytra of the latter three species are not uniform in length, nor are they evenly distributed. They are sometimes very closely spaced near the suture, about halfway between the midpoint and apices, particularly in *pensus*.

A. horni also resembles *browni* in a number of non-adult characters, that are different in *anxius* and its allies. According to Fisher (1922), the eggs of *browni* turn black before hatching as do those of *horni*. Those of *vittaticollis* darken in the same manner (Brooks, 1913). The eggs of *anxius* and *g. liragus* turn yellow or light brown prior to hatching. Barter (1957) says that *anxius* eggs are covered with a whitish liquid by the female after a group of them has been laid. None of the various workers who have observed *horni*, *browni*, and *vittaticollis* have mentioned that such a substance was applied to the eggs of those species. However, according to Mundinger (1941), *ruficollis* sometimes covers its eggs with such a substance, but often leaves them nearly naked of the covering.

After the first instar larvae of *horni*, *browni*, and *vittaticollis* bore out of the egg, they go directly to the roots of their hosts. It appears that the larvae of these species over-winter in the first instar, and generally bore much farther than *anxius* or *g. liragus* before undergoing the first molt. The latter species usually molt to the second instar soon after they enter the phloem, and their pupal chamber is often formed during the same year that the eggs are laid. Even when first instar *horni* larvae were introduced into aspen logs, they bored for long distances without molting before succumbing[1]. Apparently, for the larvae of *horni*, *browni*, and *vittaticollis*, the first molt is elicited by a very different set of conditions than are necessary for its occurrence in *anxius* or *g. liragus*.

Theoretically, at least, the most significant way *horni* differs from *anxius* or *g. liragus* is in its mode of host selection. *A. anxius* and *g. liragus* live on decrepit hosts, and seem to be attracted to them by odors given off as a consequence of the biochemical deterioration associated with decrepitude. On the other hand, *horni* seems to depend upon thigmotactic means for distinguishing poplar suckers of suitable sizes from unsuitable ones which are apparently no more or less vigorous.

Hybrid crosses between *anxius*, *g. liragus*, and *horni* were made, but do not seem to substantiate other evidence concerning their phyletic relationships. The following crosses yielded viable eggs: ♂ *horni* X *anxius* ♀, and the reciprocal; ♂ *horni* X *g. liragus* ♀[2]; and ♂ *g. liragus* X *anxius* ♀ (no reciprocal eggs).

First instar larvae of all crosses yielding viable eggs were introduced into aspen and birch logs. Some larvae of all hybrids developed at least partially. However, late-instar galleries were formed by ♂ *anxius* X *g. liragus* ♀, and one ♂ *horni* X *g. liragus* ♀ imago emerged. This one hybrid beetle, a female, has characteristics of both parental species. The ovipositor is of the normal length for *g. liragus*, and the elytra bear a pair of faint efflorescent spots. On the other hand, the marginal sclerites of the abdomen are uniformly pubescent and the pronotum has a distinct cupreous tinge, which are *horni* traits. This hybrid was fully receptive to *horni* males, but unreceptive to *g. liragus* males. The only abnormality noticed was a possible deformity in the articulation of the tarsal claws. However, it is not absolutely certain that their condition is really abnormal because the claws were not examined before the hybrid died and had dried out.

If the conclusions regarding the phyletic positions of *horni* and *g. liragus* had been drawn before the hybridization tests were performed, inviability of the eggs would have been expected. The successful rearing of a ♂ *horni* X *g. liragus* ♀ adult is a rather baffling perplexity. However, the success of this cross seems no more phenomenal in view of its wideness *per se* than it is in light of the known differences in the chromosome numbers of *horni* and *g. liragus*.

It is possible that *A. olivaceoniger* Fisher is related to *browni* and *horni*. Although *olivaceoniger* lacks prehumeral carinae, *browni* has only a trace of them. The form of the *olivaceoniger* tarsal claws is intermediate between the *browni* and *horni* forms. In most other features, all three are very similar. Nothing certain is known of the biology of *olivaceoniger*. Blanchard (1889), calling it the olivaceous variety of *acutipennis*, said it occurred on poplar sprouts in

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[1] The work of Engel (1968) seems to indicate that the behavior of *horni* larvae can be similar to that of the larvae of *g. liragus* or *anxius*, depending upon host condition.

[2] The reciprocal of this cross could not be assessed because no *horni* females were receptive to *g. liragus* males.

Massachusetts. Frost (1912), on the other hand, claimed to have encountered it quite often on oak, which would indicate that it may really be related to *acutipennis*.

Fisher (1928) places *olivaceoniger* near *criddlei* and *acutipennis*. While *acutipennis* appears to be related to *bilineatus* and allies (fig. 44) and lives on *Quercus* spp., *criddlei* lives on willows and is related to the *Salix* borer group. However, *criddlei* is not placed in the latter group because it has traits which also indicate a relationship to *horni* and its allies.

Because *criddlei* is a gall-former, its mode of host selection may be similar to that of *horni*. The habits of the larvae are more like those of *horni* than those of species in the *Salix* borer group. During the earlier stages of development, the *criddlei* larvae spiral in the phloem, but they later feed mostly within the xylem (cf Wong and McCleod, 1965).

A. criddlei resembles *horni* in having a deep, smooth median groove on the first and second abdominal sternites of males. Of the forms in the *Salix* borer group, *quadriguttatus quadriguttatus* has the strongest abdominal groove, but it is not as well-developed as in *criddlei*. This groove is weakly developed in males of *q. niveiventris* and *q. fulminans*, but absent in *A. guerini* Lacordaire, a Eurasian species (see Stepanov, 1954).

The male and female genitalia of *criddlei* are very similar to those of *horni*, although the apex of the *criddlei* penis is acuminate (fig. 45) instead of rounded as in horni. The penis apex of *quadriguttatus* and subspecies is acuminate like that of *criddlei*. The elytra of *criddlei* and those of species in the *Salix* borer group are also very similar. In addition to having the tendency for the formation of discal spots of pubescence, the elytra of all of these species are angulate at the apex (fig. 46a, b). This latter feature of the elytra appears to have reached its maximum development in *guerini*, which has greatly prolonged elytral apices with a very deep notch between them (fig. 46b).

The Nearctic *Salix* borers have well-developed prehumeral carinae. These carinae are not strongly developed in *criddlei* and are only rudimentary in *guerini*. The evidence suggests that *criddlei* may be a rather direct descendent of the form ancestral to the triad of groups composed of the *Salix* borers, *Populus* borers, and *Alnus*-*Betula* borers.

The Salix Borers. Of this latter triad, the *Salix* borers seem to be the least specialized. According to several accounts of its larval habits, *guerini* usually bores in the upper branches of willows (Gaudin, 1921, Lecomte, 1925; Horion, 1955; Lundberg, 1962), and its larval habits are quite analogous to those of *pensus*. The larval habits of the other species of *Salix* borers are essentially unknown. The size of the willows which serve as hosts of *q. niveiventris* and *q. fulminans* (e.g. *Salix lasiandra* and *S. lasiolepis*) suggests that these *Agrilus* may have larval habits quite similar to those of *guerini*. It does not seem likely that the larval habits of nominal *quadriguttatus* would differ markedly from those of its other subspecies, but the former has as its host the black willow (*S. nigra*)[1], a very large tree at maturity. Therefore, *q. quadriguttatus* could have habits analogous to those of *anxius* or *g. liragus*.

Agrilus yamawakii Kurosawa is a Japanese species (Honshu, Shikoku, Kyushu), which shows some resemblance to the Nearctic *Salix* borers. The figure in Kurosawa (1957) shows a rather unusual undulate band subapically on the ely-

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[1] In reference to *q. quadriguttatus* Fisher (1928) said: "This is probably the species recorded as having been collected on partly dead alders (*Alnus* sp.), although no specimens have been examined which were collected on that plant." This is an obvious reference to the statement of Blanchard (1889) regarding the series from which Horn (1891) described *pensus* (*granulatus*, *sensu* Blanchard [1889]).

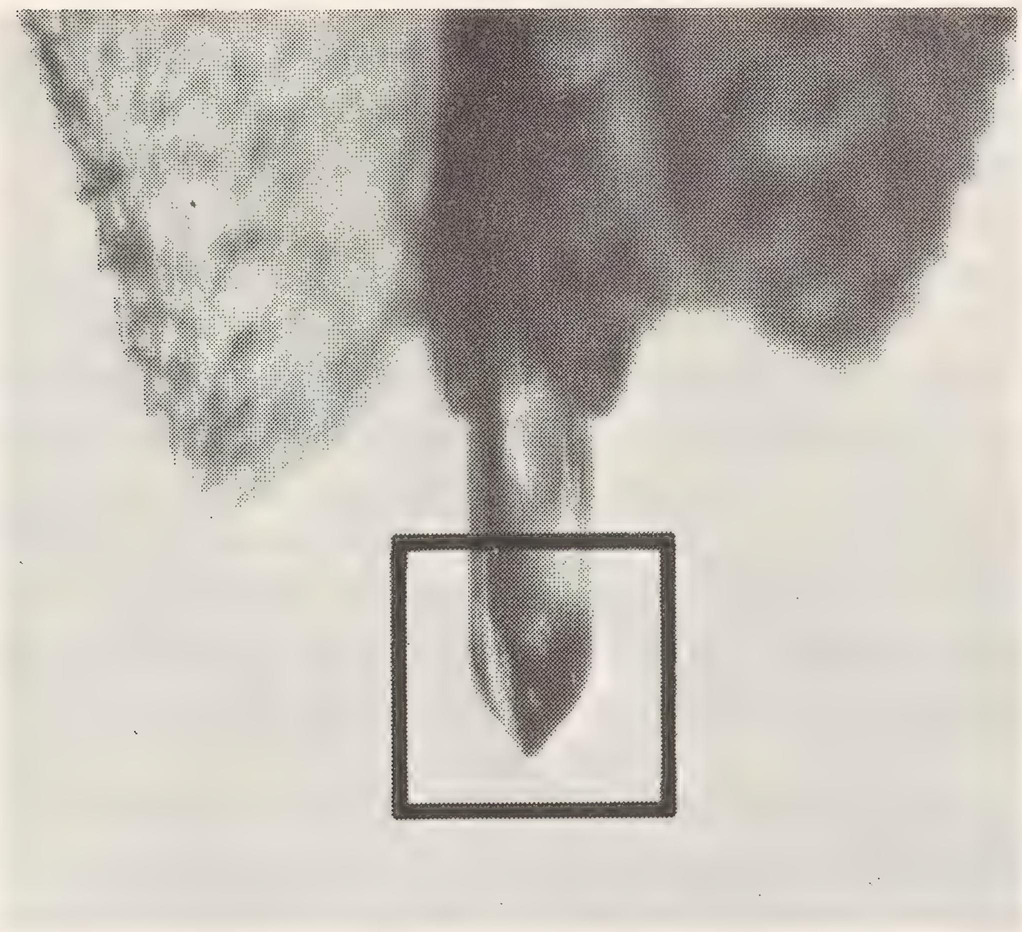

Fig. 45. Penis apex of Agrilus criddlei.

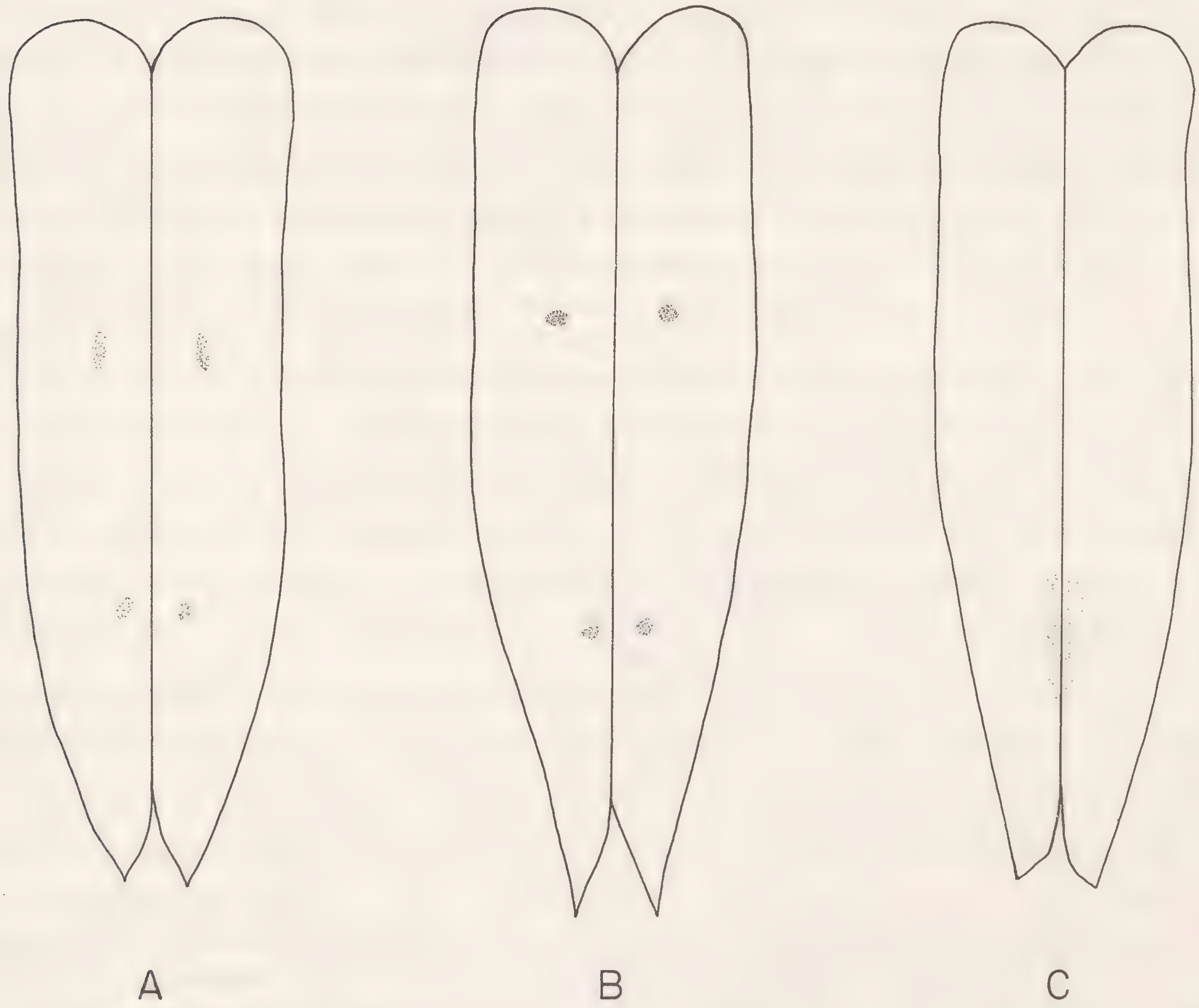

Fig. 46. Elytra of Agrilus ater (A), A. guerini (B), and A. quadriguttatus niveiventris (C). Figures of ater and guerini redrawn from Théry (1942).

tra of *yamawakii*, and there is no mention in its description of a median basal groove on the abdomen of males. However, its habitus is otherwise so much like that of *quadriguttatus* and subspecies that it is included as a possible member of the *Salix* borer group.

Agrilus guerini is the only Palearctic species in the *anxius* group that has been reared from willows. On the basis of its discontinuous east-west distribution in Europe, Horion (1950, 1955) considers it to be a postglacial relict of a tropical group. Théry (1942) comes to similar conclusions because of the peculiar form of the elytra. To be sure, there are a number of tropical forms with elytra similar to those of *guerini* (see Obenberger, 1957), but they do not appear to be at all related to *guerini* as they lack the pygidial spine. The type of *A. nevadensis* Horn, which is a synonym of *q. niveiventris* Horn, has elytra prolonged somewhat like *guerini*, but those of *guerini* are longer and more arcuate on the inner margin.

The Alnus-Betula Borers. The *Populus* borers and the *Alnus-Betula* borers probably arose independently from a *Salix* boring ancestor. Moreover, it is highly unlikely that the switch from willows to a host in the birch family could have been made by a specialized form similar in habits to *anxius* or *g. liragus*. There would, in theory, have been obstacles to its occurrence in this way. Host selection of *anxius* and *g. liragus* seems to be strongly reliant upon airborne by-products of biochemical degradation from hosts that are injured or under severe physiological stress. Although an attempt will be made later to discredit the assumption that *anxius* and *g. liragus* are closely allied and that there are no intermediate species, let it be assumed for now that the assumption is valid. In addition, let it be assumed that *anxius* was derived from a *Populus* borer, although the direction of the change is immaterial to the development of the theoretical case[1]. The foregoing assumptions yield three anomalies. (1) The *Populus* borer ancestral to *anxius* would have to be preadapted for detecting those chemical substances of birches that would indicate the equivalent of the conditions it was adapted for on *Populus*. (2) Implicit in the definition of pre-adaptation is the necessity that the foregoing occurred in the absence of *Betula* spp., but the latter presently occur in most of the areas where *Populus* spp. are found. (3) The alternative to a hypothesis of preadaptation is for the capacity to recognize equivalent conditions in *Betula* to have developed gradually in the *Populus* borer. Those accepting this hypothesis are left with the problem of explaining a sudden discontinuity (sympatric speciation) in the flow of genes between the *Populus* borer and the newly-developing population of the *Betula*-boring form. Explaining the irreversibility of the *Populus*-to-*Betula* transition is also problematical.

It is much more logical to theorize that the switch was made by a form much less specific to host conditions, and more specific to certain parts of a host (e.g. certain sizes of limbs, or limbs versus trunk, etc.). Chemo-sensory recognition of the host is not as crucial a matter in this case, allowing a little more opportunity for evolutionary trial and error. Besides one has a possible transitional form, or a fairly direct descendent of it, in *Agrilus pensus*.

Barter and Brown (1949) have suggested the *pensus* is allied with *g. populi* Fisher, but their resemblance is merely superficial. The similarity of the coloration in these two forms may reflect, in part, adaptation to somewhat similar climatic conditions for their adult life spans, even though they occur on opposite sides of the continent. The *pensus* aedeagus is unlike that of *g.*

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[1] Smith (1949a) suggested the reverse (i.e. that *g. liragus* was derived from *anxius*.

populi or g. liragus, contrary to Barter and Brown (1949). Although few g. populi males with the genetalia extruded were seen, we have examined the genetalia of many g. liragus males. The aedeagus of pensus is actually more like that of anxius than that of g. liragus (see figs. 5 & 8, above).

Agrilus pensus is related to anxius and has some subtle traits which also link it with the Salix borers. The head is often flattened or broadly impressed on the vertex as in q. niveiventris and the apices of the elytra often resemble those of the Salix borers. About halfway between the midpoint and apices of the elytra and near the suture, quadriguttatus and its subspecies often have an elongated maculation formed by closely spaced pubescence (fig. 46c, above). A similar maculation occurs in pensus (fig. 4c, above). The ecological similarities of alders and willows also render strong support to the hypothesis that the transition from the Salicaceae to the Betulaceae was achieved by a species from which pensus has descended rather directly. Figure 44 shows a Salix boring species engendering an Alnus-Betula borer later than the evolution of a Populus borer from a Salix borer. We postulate this because there are no records suggesting that the Alnus-Betula borers are not endemic to the Nearctic region.

The Populus Borers. There are, on the other hand, a number of Eurasian forms in the Populus borer group. One of them, A. ater L., may be more closely allied to the Salix borers than any of the other Populus-boring forms. Nevertheless, the listing of willow as a host for ater by Horion (1955) and other taxonomists has dubious reliability. We have never seen a reference which either cites a particular worker as having reared ater from willow or gives other rearing records. One must be skeptical of these unverified records for ater, because they may very well be referrable to guerini instead. The biology of ater is discussed by Krogerus (1922) and Kangas (1942a, b); it appears to have habits roughly analogous to those of Nearctic Populus borers.

A. ater males do not have a median groove on the basal abdominal sternites. In this respect ater appears to resemble guerini. In species which have an abdominal groove, it appears to function in properly aligning males during the act of probing and insertion of the aedeagus. In ater and guerini, the development of very sharply pointed elytral apices the enlargement of the notch between them, may have functionally supplanted the abdominal groove of males. The pointed elytra and absence of an abdominal groove in both species could indicate a rather ancient relationship and a rather direct descent from the pair of allied species proposed as the primordial Populus and Salix borers. However, the elytra of ater are shaped much like those of other Populus borers, while those of guerini appear to be an elaboration of the usual Salix borer type. Therefore, the extreme acuteness of the elytral tips and the associated loss of the male abdominal groove may be convergent developments in these two species. It is unlikely that the shape of the elytral apices bears any functional relationship to physical characteristics of the host. Hence, the consistent difference in the elytra of Salix and Populus borers should accurately reflect phyletic relationships.

Stepanov (1954) names poplars as hosts for A. fleischeri Obenberger, A. ater juriceki Obenberger, and A. tamanukii Stepanov. He says that A. tscherepanovi Stepanov lives on Populus laurifolia, which is grouped with the balsam poplars. If A. fleischeri coreicus Kurosawa, A. fleischeri nipponicola Kurosawa, and A. fleischeri kurosawai Obenberger have been properly classified as subspecies of fleischeri, they are also Populus borers.

A. tamanukii probably relates more closely to Nearctic Populus borers than other Eurasian forms. Like the Nearctic forms it has a median groove on the basal abdominal sternites of males[1]. It was described from southern Sakkhalin, which, according to Tatewaki (1963), has a mixture of temperate east Asiatic and subarctic phytogeographic elements. Therefore, this species is an ecological counterpart of the Nearctic g. liragus and it is entirely possible that tamanukii should also be ranked as a subspecies of granulatus.

Three Taiwanese species, which also have a male abdominal groove, are put in the Populus borer group only on the basis of their descriptions. They are A. subcuneiformis Kurosawa, A. satoi Kurosawa, and A. semiaurovittatus Kurosawa. These species could be ecologic analogs or homologs of g. granulatus and g. populi.

Obenberger (1958) believed that more aberration and subspeciation has occurred among Paleartic buprestids than in those of the Nearctic region. Nevertheless, it seems unlikely that the number of Eurasian species and subspecies of Populus borers could be as great as the number of available names. The number of names needed for them will probably be reduced by synonomy in the future.

Zoogeography

ASSUMPTIONS

Effect of Climatic Change. The climates to which each of these Agrilus taxa are now adapted are probably similar to those in which they diverged from their closest allies. Climatic change undoubtedly led to much of the geographic fragmentation precursory to their speciation and subspeciation. The necessity of geographic isolation for speciation is generally acknowledged; models for sympatric speciation, except in a few special cases, appear unsupportable (Mayr, 1963).

Deevey (1949) says "the occurrence of closely related species in the same area implies their differentiation in previous isolation; this isolation must have lasted long enough, first to produce the reproductive divergence necessary to avoid swamping of one by the other, and second to produce the ecologic differentiation (differences in food habits, temperature preferenda, etc.) necessary to avoid too stringent competition. Nearly all well studied cases of subspeciation and speciation point to the Pleistocene as the time of previous isolation, and the occurrence of closely related forms in the same area is therefore attributed to post-Pleistocene alterations in geography and in biogeography."

One must certainly expect exceptions to such a sweeping generalization as this. However, the pitfalls to be encountered in its application are fewer than are met with in trying to decide which pairs of species are really siblings and which are not. Indeed, the important factors contributing to recent speciation and subspeciation among Nearctic forms in the Agrilus anxius group seem to have been the changing positions of glaciers, deserts, and prairies in relation to forested areas and mountain ranges.

Pigmentation. Coloration, for the Agrilus in question, appears to be mostly a matter of climatic adaptation as opposed to being cryptic. The results of studies among other groups of insects have interesting parallels which are

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[1] Neither Stepanov (1954) nor Kurosawa (1954) seem to have recognized this as a male character, and may, consequently, have described males and females of the same species under different names.

probably meaningful. Dobzhansky (1933) found that in certain Coccinellidae there is a marked concentration of scarcely pigmented varieties in Turkestan, Iran, California, and Mexico. The further a region is removed from these centers, the darker is the average type of population found therein. The darkest forms were found in eastern Siberia. Dobzhansky acknowledges a general agreement of his findings with Allen's rule, which according to him is more properly called Gloger's rule. This rule relates depigmentation of animals to arid regions, and pigment accumulation to humid regions.

Netolitzky (1931) derived similar kinds of rules from studies of Carabidae. He relates variations in pigmentation more to differences in altitude and latitude than to humidity. According to his findings, pigmentation of European carabid beetles increases with increasing altitude and latitude.

Kalmus (1941) gives some working hypotheses (he calls them laws) regarding pigmentation that are more elaborate and combine some of the features of Gloger's rule with those of Netolitzky's rules. He starts from a set of theoretical premises which are based upon the structure of insect cuticle and the attributes associated with the nature of its pigmentation. Kalmus says, "darkening and hardening of the cuticle are one in the same process." Whether or not this is entirely true is still a controversial matter (Cottrell, 1964). Kalmus (1941) attributes several different functions to hardening and darkening. He maintains that the functional attributes of the cuticle which are enhanced with increasing hardening and darkening are (1) heat absorption, (2) protection from high frequency radiations (i.e. ultraviolet), and (3) moisture retention.

There seems to be no logical reason for contesting the validity of the assumption that dark cuticles are more heat-absorbent than pale ones, and it is supported, in a small way, by the experiments of Buxton (1924). Kalmus (1941) generalizes that if the mode of life of an insect makes heat absorption advantageous, its coloration will be dark; if heat absorption is irrelevant or disadvantageous it may be pale. He also maintains that melanic forms are found at high altitudes because their dark cuticles give them greater protection from high frequency radiations. This may be true, but the effects of increasing high frequency radiation and those of decreasing temperature with increasing altitude cannot be mutually exclusive. His suggestion that insects exposed to drought are dark seems to be antithetic to Gloger's rule. Moreover, it might be contradictory to relate hardening and darkening to aridity were it not for the fact that iridescence is often associated with aridity. Many arid regions are also hot, but iridescence would seem to be compensatory; according to Kalmus (1941) it is associated with darkened cuticles, and gives them the heat absorbing qualities of pale coloration in combination with the moisture retaining capabilities accompanying heavy sclerotization.

Fisher (1928) was not cognizant of the close alliance between *q. quadriguttatus* and *q. niveiventris*, but thought that each of these *Salix* borers was related to its sympatric *Populus*-boring counterpart, *g. granulatus* and *g. populi*, respectively. The color resemblance of each *Salix* borer to the *Populus* borer living with it is close enough so that they were usually lumped as single western and eastern species prior to Fisher's revision. While *granulatus populi* and *quadriguttatus niveiventris* are iridescent reddish-cupreous above (the latter sometimes very dark), the nominate subspecies are duller, being more or less dusky olivaceous to reddish-fuscous. These pairs of *Populus* and *Salix* borers seem to be the most austral and least alpine of the forms in the triad composed of the *Salix*, *Populus*, and *Alnus*-*Betula* boring species.

The climatic affinities of *anxius* and *g. liragus* are quite boreal and alpine by comparison. They are darkly pigmented, usually almost black, although the pronotum and vertex of *anxius* are apt to be cupreous, particularly in specimens from the northeastern *U. S. A.* and southeastern Canada. Fisher (1928) failed to distinguish *anxius* from *g. liragus* because they are very similar.

The similarities within any of the sympatric pairs, *anxius* and *granulatus liragus*, *quadriguttatus niveiventris* and *granulatus populi*, or nominate *quadriguttatus* and *granulatus*, are homoplastic[1], not homologous. They appear to be due to adaptation to similar or equivalent climatic conditions.

DISCUSSION

Faunal Connections. The gradual cooling of climate that occurred at the close of the Tertiary, particularly at higher latitudes, brought southward retraction of the Arcto-Tertiary flora and largely eliminated it from Europe (Spurr, 1964). Remnants of this forest persist in eastern Asia (Japano-Manchurian), Pacific coastal North American (Vancouveran), and eastern North America. North of these Arcto-Tertiary remnants, particularly in the more continental regions, the modern boreal forest associations were formed (Linsley, 1963). Logically, then, one looks to the Japano-Manchurian region for faunal connections with the Vancouveran and Alleghenian regions. Linsley (1963) shows that the cerambycid faunas of the latter two regions have separate connections with the former. Species bridging the gap between *browni* and *horni* or between the latter and *criddlei* may occur in the Japano-Manchurian region. In this same region one might also find pre-Quaternary connections with the non-boreal *Salix* and *Populus* borers of North America (cf p. 82). These non-boreal forms may be rather direct descendents of the pre-Quaternary forms which presumably gave rise to the boreal ones, such as the *Populus* borers, *tamanukii* of eastern Asia, and *g. liragus* of North America. Each of these boreal *Populus* borers could have had an independent origin but there is no necessity for assuming that it was so.

Linsley (1963) says that Holarctic cerambycid species dominate in the forests of such boreal derivatives of the Arcto-Tertiary Geoflora as the northern and high elevation Pinaceae, and the northern deciduous trees, especially *Salix* and *Populus*. There is a definite likelihood that *tamanukii* is conspecific with *granulatus*. In fact, *tamanukii* and *g. liragus* may represent derivatives of a single boreal form which might have persisted at the southern edge of the Bering Arc during late-Pleistocene glacial maxima.

Subspeciation. It is clear that *g. liragus* must have been isolated from *g. granulatus* and *g. populi* (or the *g. granulatus*-*g. populi* ancestor) in an area of colder climate, where it derived a more cold-adapted type of pigmentation and its affinity for a boreal climate. There is no logical explanation for isolation north of the *g. granulatus*-*g. populi* range unless it occurred as a result of glaciation or unless *g. liragus* was absent from North America and derived its boreal affinities in Asia, later migrating to North America through Beringia. In the latter case, the problem of isolation from Japano-Manchurian forms is raised.

According to Heusser (1965), macro-fossils, dated 35,000 B. P., from the unglaciated Alaskan interior, show that a forest of aspen, birch, and spruce persisted there throughout the Wisconsin glacial interval. This refugium seems to be the only northern Nearctic one (other than Vancouver Island) for which

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[1] "Homoplasy is resemblance not due to inheritance from a common ancestry (Simpson, 1956)."

there is good evidence of the survival of forests during the Wisconsin glacial maxima. This seems to be as likely a place as any for the derivation or reinforcement of the boreal affinities of g. liragus. As suggested above, another possible refugium is the southern edge of the Bering-Chukchi platform which was emergent during glacial maxima. Although most paleobotanists who have studied the problem suggest that forests never existed on the Bering land bridge, their views do not seem to be supported by the frequency of Holartic distributions among boreal forest insects.

A. granulatus liragus occurs at the same latitudes with g. granulatus or g. populi in mountainous regions, and in these areas the former seems to be confined to higher altitudes, while g. granulatus or g. populi occur mostly in river bottoms at lower altitudes. Their coloration appears to be a genuine indication of their climatic affinities. Intergradation between g. liragus and the other subspecies should occur at intermediate altitudes where cottonwood (P. deltoides) or black cottonwood (P. balsamifera ssp. trichocarpa) occurs together with aspen (P. tremuloides).[1]

One specimen from Crow Agency, Montana (July, 1916; R. K. Kellog), recorded under Agrilus granulatus by Fisher (1928), appears to represent an intergrade between g. granulatus and g. liragus, as its color is rather dark and the spots on the elytra are not as distinct as those of g. granulatus specimens from farther south. The Agrilus granulatus[2] discussed by Brown and Stevenson (1963) are very similar to the foregoing. It is interesting that the species of the various sections of the genus Populus hybridize in southern Alberta, where their habitats intergrade (Brayshaw, 1965). For g. granulatus and g. liragus this area seems to represent a natural counterpart of the "hybridized habitat" of Anderson (1948).

During the Pleistocene pluvials--the cool, moist periods when glaciation occurred--the ranges of willows and cottonwoods must have expanded from both east and west out into the southern Great Plains so that there was even less disjunction than occurs presently. Although they do not show Salix and Populus, the pollen analyses of Martin and Mehringer (1965) for the southwestern U. S., indicate that this is more than just a likelihood. Thus, the stage would have been set for movement of eastern Salix and Populus borers into the West and vice versa. Following continent-wide dispersal of these forms, there may have been a sequence of hypsithermal divergences followed by broad intergradations between eastern and western forms during pluvial periods. It is very likely that this occurred several times, as Deevey (1949) says that in the history of Lake Bonneville there have been two, perhaps three, major late-Pleistocene pluvials.

At the present time the ranges of g. populi and g. granulatus do not appear to interdigitate extensively. That of g. populi is western, extending from southern California to British Columbia and as far east as Missoula, Montana. The range of g. granulatus extends from the Great Plains eastward; although its limits are not well-known, Fisher recorded it from as far north as Nassau, New York, and as far west as Crow Agency, Montana, and south to Illinois and

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[1] Any Populus sp. or cultivar appears suitable for all of the subspecies of granulatus, provided that the former occur in habitats of the latter.

[2] Specimens from these rearings are deposited in the Canadian National Collection, Ottawa, Ontario.

Missouri, and there is one specimen from North Carolina in the Horn collection[1]. In Colorado only *g. granulatus* is known, but some of the specimens[2] examined from that area show indications that the two probably meet and intergrade there in places.

The *Salix* borers *q. quadriguttatus* and *q. niveiventris* are known from farther south than their *Populus*-boring counterparts. The range of *q. quadriguttatus* extends roughly from Georgia[3] to Texas, north to Colorado and east to Pennsylvania and Washington, D. C. The northern range limit of *q. niveiventris* lies just south of Placerville, California (see below) and, according to Van Dyke (1942), this subspecies ranges south into Baja California, and east into Arizona and New Mexico. Although we have seen no definite *q. niveiventris*-*q. quadriguttatus* intergrades, some *q. quadriguttatus* specimens are distinctly tinged with red, probably indicating recent genetic exchange with *q. niveiventris*. The divergence between these *Salix* borers was probably concurrent with that occurring between *g. granulatus* and *g. populi*.

Because of their color similarities, it appears that *quadriguttatus niveiventris* and *granulatus populi* were confined to regions with similar climates during their period of divergence (hypsithermal) from eastern allies. Their ranges at that time may have been more nearly coextensive than at present. Although *q. niveiventris* occurs in Baja California, Arizona, and New Mexico, *g. populi* has never been collected in these areas, in spite of the occurrence of Freemont cottonwood (*Populus freemontii*) in their stream bottoms. On the other hand, *g. populi* occurs undifferentiated well north of *q. niveiventris*, where *quadriguttatus* is represented by the more northern subspecies, *q. fulminans*.

According to Van Dyke (1942) some records for *q. niveiventris* from British Columbia may refer to *q. fulminans*, but this is not altogether certain because *g. populi* was not distinguished from *q. niveiventris* any sooner than *q. fulminans*. We are not aware of any reliable records for *q. fulminans* outside of those for Oregon and Northern California, and do not know how well-differentiated *q. niveiventris* and *q. fulminans* are. Unfortunately, Fisher (1928) described *q. fulminans* from a series of specimens which seem to represent intergrades[4] between *q. niveiventris* and *Salix* borer populations north of the *q. fulminans* type locality. This series (*q. fulminans* type and paratypes) was taken at Placerville, California, and some specimens are iridescent reddish cupreous above, which seems fairly typical for *q. niveiventris*, while others are greenish. Fisher (1928) had specimens from Biggs and Castle Crags in California which were strikingly different from those collected farther south at Placerville. He

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[1] Philadelphia Academy of Sciences, Philadelphia, Pennsylvania.

[2] Personal collection S. G. Wellso, Dept. of Entomology, Michigan State University, East Lansing.

[3] Record in Franklin and Lund (1956).

[4] Fisher based his distinction of *q. fulminans* upon the efflorescent spots on the sides of the abdominal sternites, but this character does not seem to merit the value he has given it and may be more characteristic of the population at the type locality than than of those elsewhere.

says, "the specimens from Biggs have the elytra dark green and the pronotum more bronzy green, and two specimens from Castle Crags[1]......, which I have placed under this species, have the pronotum greenish blue and the elytra a beautiful violaceous blue." Specimens were seen from Crescent Mills, California, in the northeastern part of the Sierra Nevada, that are bright apple-green. Barr[2] said he had examined relatively few specimens of this Pacific Northwest form, but those he had seen are green. Beer[3] said q. fulminans specimens from northern California and Oregon are blue.

Some sort of past range disjunction must account for the color differences of q. niveiventris and q. fulminans. It may have occurred during a hypsithermal period, when the ancestral populations in the Cascades or northwestern coast ranges may have been isolated from those in the southern coast ranges or the Sierras. An alternative possibility is that the population that gave rise to q. fulminans may have been isolated in a Pacific Northwest glacial refugium, such as the one which, according to Heusser (1960), existed on Vancouver Island. The nature of the climatic affinities of q. fulminans may become clearer as more collections are made.

The Multiplication of Species

Speciation in the anxius Group. The only cases of complete speciation among the triad of the Populus, Salix, and Alnus-Betula borers that can, with reliability, be designated as Nearctic, Pleistocene events are those which led to the derivation of the ancestor of the latter and the subsequent formation of two siblings from it. Previously (page 80) we discussed the possible derivation of the ancestral form from a willow feeder. This may have occurred very early in the Pleistocene, and the point of origin may have been eastern North America. No species in the anxius group, other than its namesake, is known to live on a species of Betulaceae in the western part of the continent. However, Chamberlin (1924) says he collected a specimen of q. niveiventris on Oregon alder (Alnus rubra) near La Grande, Oregon, and that a series was collected on black cottonwood and Oregon alder at Oakridge, Oregon.

Following his description of g. populi, Fisher (1928) lists 4 of the paratypes as having been taken on Oregon alder by Chamberlin at Oak Ridge, Oregon[4]. The only one of these paratypes remaining in the collection of the U. S. National Museum has no host label. One in the Chamberlin collection at the California Academy of Sciences, was labeled "Oakridge VI-29 Ore./Populus trichocarpa/ W. J. Chamberlin Collector[5]." Chamberlin (1929) described trichocarpae, a synonym of g. populi from the same series of Oak Ridge specimens, but he did

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[1] Emendation of his "Castle Crag."

[2] Personal communication, 1967; W. F. Barr, Dept. of Entomology, University of Idaho, Moscow.

[3] Personal communication, 1967; F. M. Beer, Dept. of Biology, School of Science, Oregon State University, Corvallis.

[4] Emendation of Fisher (1928) who cites Oak Ridge as a California locality.

[5] Personal communication, 1967; H. B. Leech, California Academy of Sciences, San Francisco.

not say any of these were collected on alder (cf above citation, Chamberlin, 1924). Beer and Hatch (1941) cite lombardy poplar, black cottonwood, and Oregon alder as g. populi hosts, but are, no doubt, following Fisher (1928).

Beer[1] doubts the existence of a western form resembling g. populi that infests Oregon alder. He has collected g. populi in places where alders and black cottonwoods had been felled simultaneously, but saw none on the alders. Moreover, he says, "Knowing Chamberlin's inaccuracies on host plants--in fact his general failure to mention this feature would prompt me to discount completely occurrence on this plant [alder]."

Evidently anxius has a greater specificity than pensus for hosts in a severely weakened condition, but anxius hosts are usually also larger and more likely to occur on xeric sites. A. pensus, then, appears to be more "primary" in its attacks on alders and young river birches than anxius is in attacking its hosts. There is no á priori reason for assuming that anxius would not be attracted to large felled or injured river birches, provided they were located in the right places. A number of birches appear to be satisfactory for anxius, and the alleged olfactory attractants, therefore, appear not to be so host-species-specific as they are specific to certain conditions of the host. On the other hand, there is no evidence to show that pensus is not attracted to such large felled or injured river birches, but without such evidence one must assume that it is not. It seems very necessary to hypothesize this and the other anxius-pensus differences proposed above, if one is to explain their discreteness in sympatry.

The distribution of Agrilus pensus suggests that it was confined to the Atlantic seaboard during the primordial stage of its evolution. The divergence of anxius and pensus may have occurred while the latter was confined to the glacial refugium known to have existed in the southeastern U. S. There is evidence showing that about 15 to 16 thousand years ago forests of birch and alder mixed with pine, spruce and fir, existed in the Dismal Swamp region of southeastern Virginia (Whitehead, 1965). Similar ecological conditions may have existed there during glacial ages prior to the Wisconsin so that the common ancestor of anxius and pensus may have diverged from a Salix-boring ancestor in the same refugium.

The ranges of pensus and anxius and also their color differences suggest that when they were geographically isolated they were exposed to different climatic conditions. Therefore, anxius may have been confined to a refugium west of the Appalachians in the south central U. S. Although there has been a great deal of dispute on this matter, it has become increasingly evident that during the Wisconsin, at least, boreal tree species occurred as far south as Louisiana and Texas (cf Deevey, 1949 and Whitehead, 1965).

Following its continent-wide dispersal, anxius may have had its range fractured during another glacial stage. Specimens from the East differ from western ones in having the vertex and pronotum more distinctly cupreous-colored. Specimens from the Upper Peninsula of Michigan may represent intergrades, as some are colored more like g. liragus, while the pronotum and vertex of others are quite distinctly cupreous-tinged. Townes[2] says it is not

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[1] Personal communication; see footnote 3, page 87.

[2] Personal communication, 1967; H. K. Townes, American Entomological Institute, Ann Arbor, Michigan.

unusual for intergrades between eastern and western subspecies of ichneumon-flies to occur in that area. These east-west differences of *anxius* adults could relate to the fact that the only indigenous western birches of tree size are those of the paper birch group, which are mostly boreal. Because *anxius* occurs at least as far south as Washington, D. C. in the East, adults from the West, generally, may be more cold-adapted.

The Sibling Species Concept. Mayr (1963) defines sibling species as "morphologically similar or identical populations that are reproductively isolated." Certainly, *anxius* and *g. liragus* would be sibling species by that definition, but it is of little value if it fails to make a distinction between homoplasy[1] and homology. "The fundamental difference between the method of morphological and phylogenetic systematics is that the latter breaks up the simple concept of resemblances (Hennig, 1965)."

The archaic level of *Agrilus* classification is due to the relatively unsophisticated concepts of the classifiers, who usually have not tried to distinguish between homoplasy and homology. Those unaware of this fact tend to regard *Agrilus* and other large buprestid genera as being more unique than they really are. Mayr (1963) says:

> Among the 25 species of *Carabus* beetles from central Europe, 80 percent are polytypic, while in certain well known genera of buprestid beetles not a single[2] species is considered polytypic. There are still large groups of animals in which all species are listed under binomials. It would be interesting to know to what extent this is due to lack of geographic variation in the phenotype and to what extent to insufficient taxonomic analysis. Sibling species, of course, are nearly always monotypic.

Although Obenberger (1957) claimed that the Buprestidae are taxonomically well-known, they certainly have not been studied nearly as intensively as the majority of Carabidae. Therefore, Mayr's comparison of buprestids and carabids is invalid. There appears to be no greater lack of geographical variation in the phenotypes of buprestids than in most other groups (see Obenberger, 1958). Binomial names are still preponderant over trinomials in *Agrilus* because much of the taxonomic work on that genus is old or has been done by species describers instead of classifiers. Some of it has also been done by people working on local faunas. The forms they call "*sibling species, of course, are nearly always monotypic*."

Mayr (1963) drew the following "conclusions concerning sibling species":

> 1. There is no sharp division between ordinary species and sibling species...
>
> 2. Sibling species, when subjected to a thorough analysis, usually are shown to differ in a whole series of minor morphological characters. Like ordinary species they are separated from each other by distinct gaps.
>
> 3. Sibling species are apparently particularly common in those kinds of animals in which chemical senses (olfactory and so on) are more highly developed than the sense of

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[1] Defined in footnote on page 84.

[2] Probably an overstatement of the case, with the possible exception of some smaller genera. However, Mayr (1963) does not appear to be referring to any of the smaller genera because they are obscure and because he elsewhere refers to *Agrilus* and *Acmaeodera*.

vision... Sibling species are apparently rarest in organisms such as birds that are most dependent on vision in the recognition of epigamic characters.

4. There is no indication that sibling species arise by a process of speciation different from that which gives rise to other species.

5. Degree of morphological similarity in sibling species is an indication not of genetic similarity, but rather of developmental homeostasis. A reconstruction of the genotype, resulting in the reproductive isolation of two species, can take place without visible effect on the morphology of the phenotype [cf number 2!].

6. Evolutionary changes in the genetic constitution seem to occur in groups of sibling species at the same rate as in groups of morphologically very distinct species.

The following paragraph from Mayr (1963) is certainly contradictory to numbers 4 and 6 of the conclusions listed above. He says:

> In many groups of insects there are large genera with many species, each of which appears to be limited to a single host. Genera with essentially monophagous species have been described for microlepidoptera, solitary bees, buprestid beetles (*Acmaeodera*, *Agrilus*), chrysomelid beetles (*Calligrapha*, *Arthrochlamys*), and other groups. Two phenomena in particular seem to suggest a mode of speciation in these food specialists that is different from speciation in most other animals. The first is that monophagous insects often, if not usually, belong to large genera. It is argued that sympatric speciation permits more rapid and more frequent speciation than geographical speciation. It would seem even more plausible, however, that the great number of congeneric species is due to the vastly increased number of available niches and the reduction of competition. Likewise, high food specificity should greatly enhance the efficiency of eco-geographical barriers.

Mayr seems to make analogies with speciation among insular birds, and in doing so does not seem to be in complete accord with number 3 of his conclusions about sibling species. He claims that:

> As in all speciating animals the crucial events are apt to take place in peripherally isolated populations and these have not been studied adequately in even a single one of the groups of monophagous species. As a working hypothesis one might assume that a subsidiary host may offer more favorable conditions under the changed ecological situation of the marginal environment (fig. [47]). The shift from one host to another will set up an increased selection pressure that will result in rapid genetic alteration of the population. The amount of genetic variability appears to be low in a species that has been adapted for life on a single host. Host specificity is thus an ideal prerequisite for rapid speciation.

A narrow-ranged host specificity certainly is low variability *per se*, but does not necessarily reflect low genetic variability. There seems to be no reason to assume that host specificity differs basically from other phenotypic aspects. Relatively invariable host specificities, therefore, may be a consequence of homeostasis or coadaptation of the gene pool. "The real problem in speciation is not how to produce a difference but rather how to escape from the cohesion of the gene complex. No one will comprehend how formidable a problem this is who does not understand the power of the cohesive forces that are responsible for the coadapted harmony of the gene pool [Mayr, 1963]." As far as we know, the problem of breaking away from gene pool coadaptation is greatest for species with a narrow range of host specificity because the cohesiveness of their gene pools may be greatest.

It appears that in the *anxius* group species which have highly specialized relationships to their hosts in a given respect (i. e. to species, size, physiological condition, etc.) may usually evolve from less specialized species or from

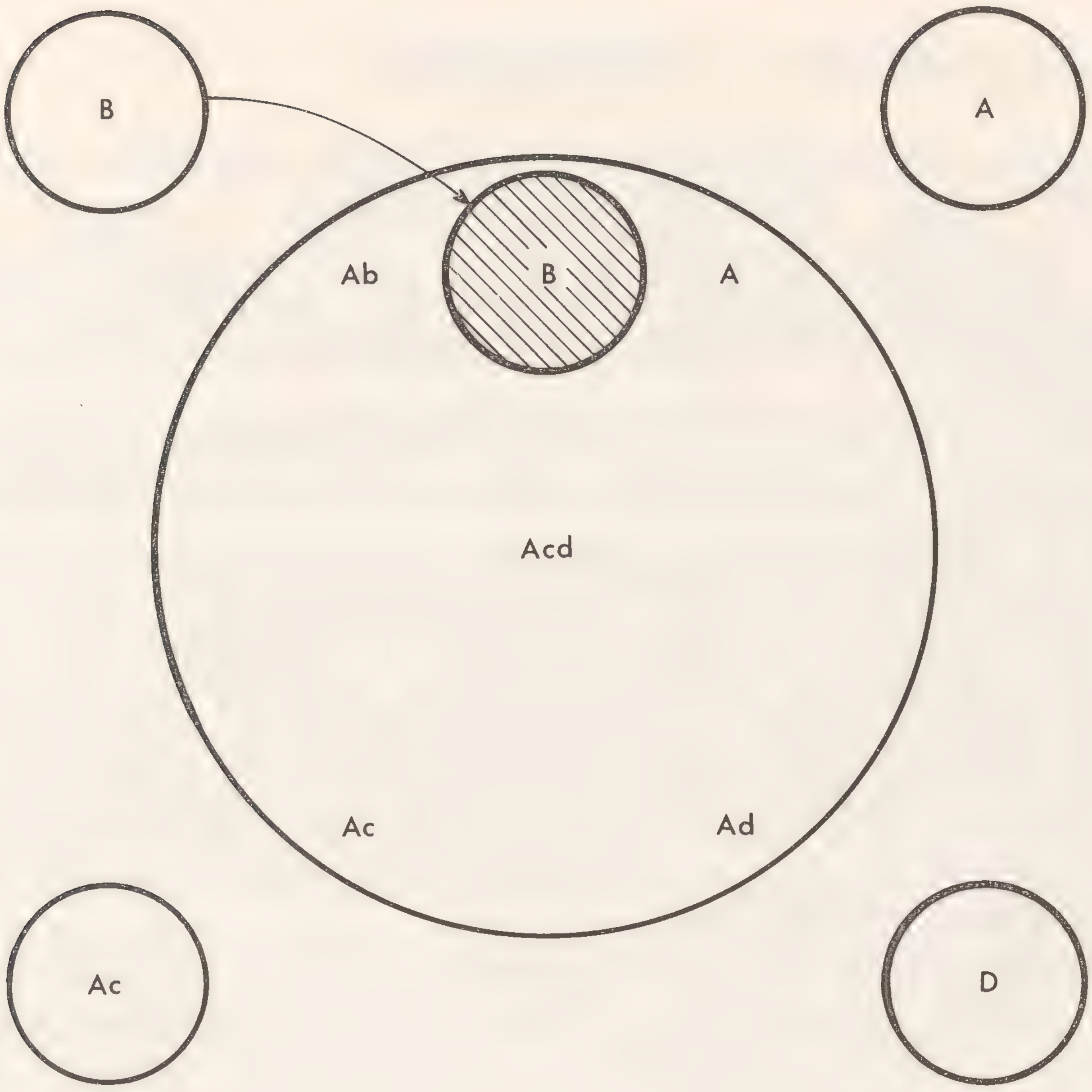

Fig. 47. Primary hosts (capital letters) and subsidiary hosts (small letters) of an essentially host-specific species. The large circle indicates the main range of the species; the outlying small circles, the peripheral isolates. New primary hosts (B, D) are acquired in some peripheral isolates, facilitating subsequent speciation. Reinvasion from the isolate that is host specific for B will establish a new species (hatched area) if reproductive isolation had been acquired during the geographic isolation (legend as in Mayr, 1963; figure redrawn).

species specialized in a different way. The most recent (mid- to late-Pleistocene) instances of complete speciation which seem to have occurred among the Populus, Salix, and Alnus-Betula borer groups (fig. 44, above) are those in which an Alnus-Betula boring species evolved from a Salix borer and subsequently gave rise to pensus and anxius. While anxius has evolved the greater specificity to physiological host condition, pensus appears to be more specific to host size.

One does not need a special working hypothesis for explaining these speciations. It is most plausible to attribute them to the events of the Pleistocene, in particular glaciation, which undoubtedly gradually severed ancestral stocks and left the disjunct populations with ranges that probably became separated farther and farther and increasingly different in climate.

Mayr's model (fig. 47) does not seem to provide for geographic separation sufficiently great to result in the climatic differences that seem to have been precursory to speciation in the anxius group, at least, nor does it seem to allow enough time for the occurrence of these climatic differences and for the reconstruction of the genotype. Perhaps in groups for which rapid speciation is a credible assumption, this model will prove to be worth considering. Most of the large groups will require a good deal more study before it will be possible to assert that conventional hypotheses are not as plausible in specific cases as are hypotheses providing for rapid speciation.

Evolutionary Synopsis

The reader is referred to figure 44 (p. 75) for a general summarization of the relationships between the forms in the *Agrilus anxius* group. The important points are these:

1) There appears to be no direct relationship between *horni* and *anxius*; while *horni* is probably most directly allied to forms like *browni*, *pensus* is the closest ally of *anxius*.

2) The major difference between *horni* and *anxius* (and allies of the latter) relates to the distinctness of their modes of (hypothesized) host selection. *A. horni* appears to rely upon a stem ''measuring'' mechanism in limiting the placement of its eggs to aspen suckers of particular sizes (but apparently without any discrimination in relation to their physiological condition). On the other hand, *anxius* oviposits on hosts that are in a decrepit physiological state and is apparently attracted to them by odiferous by-products of the bio-chemical breakdown associated with their decrepitude.

3) Forms linking these two distinct modes of life are found in *pensus* or *quadriguttatus* (and its subspecies). These species are apparently less specific to host condition and more specific to host size than *anxius*, although probably more reliant upon a subnormal state of host physiology than *horni*.

4) *A. quadriguttatus* and *guerini* probably descended from a single phyletic line, and the latter seemingly has developed some significant morphological modifications from the usual *Salix* borer type. These *Salix* borers appear to share common ancestry with: (a) *criddlei*, a gall-former living on willow, which may in turn be somewhat related to *horni*, (b) a line of *Populus* borers including the Palearctic *ater* and Nearctic *granulatus*, and (c) *anxius* and *pensus*, through a later derivation independent of that for the *Populus* borer group.

5). The sibling species concept has been applied far too indiscriminately in advance of a thorough assessment of the relationships among species, and this is certainly pertinent to many groups besides *Agrilus*. The following pairs have often been related by homoplasy (similarity) rather than homology: *anxius* and *g. liragus*; *g. granulatus* and *q. quadriguttatus*; or *granulatus populi* and *quadriguttatus niveiventris*.

6) The only recent speciations that seem evident for the *Populus*, *Salix* and *Alnus*-*Betula* borer groups are the derivation and subsequent splitting of an *anxius*-*pensus* common ancestor.

7) No special models are needed to explain these speciations or the subspeciations that have occurred in *quadriguttatus* (Nearctic *Salix* borers) or *granulatus* (Nearctic *Populus* borers). They can logically be related to biogeographical events of the Pleistocene.

SUMMARY

The principal objective of this study was to assess the relationship between *A. anxius*, *A. pensus*, *A. granulatus liragus*, and *A. horni*. This was accomplished by: (1) studying specimens, (2) assembling what was known about general aspects of their biology, augmenting it in places with new observations, (3) making behavioral observations on the adults in the field and laboratory, and (4) analyzing their phylogeny and zoogeography, relying heavily on material from the preceeding sections.

In the process of studying the taxonomy of the adults, the need for a number of nomenclatural changes became apparent. Changes which were made very recently (see Carlson, 1969) include lowering four taxa from species to subspecies status (*populi* and *liragus* to ssp. of *granulatus*, *niveiventris* and *fulminans* to ssp. of *quadriguttatus*) and the suppression of two names, *betulae* and *nevadensis* as synonyms of *pensus* and *q. niveiventris*, respectively. Herein *lateralis* is suppressed as a synonym of *ruficollis*, and the species which has been incorrectly called *lateralis* is named *browni*.

Barter and Brown (1949) distinguished *g. liragus* from *anxius*, but thought *horni* to be a probable synonym of the latter. After Harrison (1959) had discovered *horni* boring in the roots of aspen suckers, Nord et al. (1965) established its identity and showed that *horni* was clearly distinct from either *anxius* or *g. liragus*.

A careful comparison of the adults revealed that *horni* has some previously unnoticed or unemphasized morphological traits which, although they are subtle, set it apart from *anxius* or *g. liragus*. They are discussed at some length in the taxonomy section and again in the evolution section, where their significance is assessed.

These anomalous morphological characteristics of *horni* seemed to link it in some way with species which lack prehumeral carinae. A paper by Fisher (1922), completely overlooked until late in this study revealed that the habits of *A. browni* are remarkably like those of *horni*. The morphological traits separating *horni* and *anxius* or *g. liragus* and linking it with other forms, not closely related to the latter, thus became more meaningful. The important ways in which the habits of *horni* differ from those of *anxius* or *g. liragus* are enumerated below.

1) The eggs of *horni* are deposited at the bases of young aspen suckers, while suitable oviposition sites for *g. liragus* and *anxius* occur almost anywhere along the stems of larger trees.

2) After hatching the *horni* larvae bore into the phloem and proceed downward to a root and move rather directly out along it for a distance of up to 3 1/2 feet before the first molt occurs. This primary molt probably does not occur until the spring following eclosion from the egg, when the larvae may begin spiraling back toward the sucker stem. The first molt of *anxius* or *g. liragus* larvae occurs soon after the larvae bore into the phloem.

3) In many cases the larvae of *anxius* and *g. liragus* complete their development and form a pupal chamber during the same year in which eggs are laid. They thus have a one-year life cycle under some conditions and a two-year cycle under others. The usual length of life cycle is two years for *horni*, and the only exception that seems possible, is an occasional three-year cycle.

4) While *anxius* and *g. liragus* infest hosts that are under physiological stress and seem to be attracted to them by odiferous products of biodegredation, *horni* appears to distinguish suitable from unsuitable hosts on the basis of size rather than their physiological condition. The suckers on which *horni*

eggs are found seem to be of normal vigor (i. e., no different than their neighbors). Sucker diameter (as opposed to height) appears to be the most important variable correlating with the occurrence of eggs. It is, therefore, suggested that horni restricts its egg deposition to suckers within rather narrow diameter limits (0. 3 to 0. 9 inches at base) by thigmotactic means. The differences between the two kinds of host selection seem to be so extensive as to preclude the derivation of one from the other except through a series of intermediate stages.

Agrilus pensus seems to be a direct descendant of an ancestor representing one of the intermediate stages. A two-year life cycle seems prevalent, and a one-year cycle is unlikely because of the small size and thin bark of its hosts (alders and young river birches). A. pensus is probably more primary than anxius or g. liragus, although it seems likely that the hosts it attacks are under some physiological stress. Nevertheless, the average level of host resistance which pensus is subjected to should approximate the maximum encountered by anxius or g. liragus.

Host resistance is treated here as a population regulating factor, together with parasites and predators. The sinuate galleries of anxius and zigzag galleries of g. liragus appear to be mechanisms for coping with host resistance, because the galleries of either species follow a more random course in the phloem of hosts that have succumbed or are near death.

The survival of horni larvae may depend, in part, upon the ability to lower the vigor of the host through root-girdling. Their ability to significantly lower the vigor of the host by root-girdling should relate to root diameter. Because root diameter seems to correlate well with sucker diameter, the restriction of oviposition by horni to suckers with basal diameters ordinarily below 0. 9 inches is probably an indirect means for coping with host resistance.

The effects of parasites and predators as population regulating factors is more obvious, and for this reason, their significance may be overrated in comparison with that of host resistance. Woodpeckers and egg-parasitizing chalcidoids account for the greatest percentage of combined parasite and predator effects upon populations of anxius and g. liragus. The eggs of horni are parasitized rather infrequently, but larval parasites consume a very high percentage (about 42 percent) of horni brood between the late larval and late pupal stages. Some corrections are made regarding incorrect parasite rearing records.

Even though horni and g. liragus live on the same host species there appears to be no chance for interspecific mating because the males of each orient to hosts that are likely to be attractive to conspecific females. Moreover, horni females are completely unreceptive to liragus males, at least in the laboratory, and this seems to partially preclude hybridization in chance encounters. It appears, that g. liragus males have lost some subtle facet from their courtship behavior repertoire. A. anxius females are occasionally receptive to g. liragus males, but horni females, nevertheless, seem quite receptive to anxius males. This seems to put the male-to-female communications of anxius somewhere intermediate between those of g. liragus and horni, as horni males are accepted readily by females of either anxius or g. liragus. A. anxius could be intermediate in this respect because of the relative propinquity of its ancestry to species that live on willows as compared to that of g. liragus.

Males show no disinclination to court females of other species in the laboratory. Moreover, males do not even appear to recognize the sex of the individuals they court until they have made physical contact with them. Sexual recognition by males appears to depend upon the structure of the courted individual's last abdominal segment. That segment is sexually dimorphic, and after a courting male probes it with his aedeagus he leaves males but prolongs courtship even with unreceptive females. This seemingly inefficient mode of sexual recognition appears to be homostatically tied to a dispersing function for homosexual encounters between the quasi-territorial males.

The interpretation presented here concerning evolutionary relationships within the *Agrilus anxius* group, contrasts with views held by earlier students. For example, *horni* is not considered as being a close ally of *anxius* or *granulatus liragus*. *A. horni* and *browni* have very similar habits, and these species appear to be more closely related to each other than to other species. This interpretation leaves a distinct phyletic gap between *horni* and *anxius* or *g. liragus*. Intermediates which seem to fill this gap are *criddlei* and a group of willow boring species that includes *quadriguttatus*. The ancestors of the latter group seem to have given rise first to a phyletic line that includes *g. liragus* and later to one including both *anxius* and *pensus*. The derivation of the line including *anxius* and *pensus*, and its subsequent splitting seem to be the only recent (mid- to late-Pleistocene) cases of complete speciation for the part of the *anxius* group considered in detail.

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*See table of contents, where each of the four principal taxa are sometimes listed by their common names: the alder-birch borer (_pensus_), the aspen root girdler (_horni_), the bronze birch borer (_anxius_), and the bronze poplar borer (_granulatus liragus_).